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Latest Ordovician to Earliest Silurian Colonial Corals of the East-Central United States

by

Graham A. Young
and
Robert J. Elias

Paleontological Research Institution
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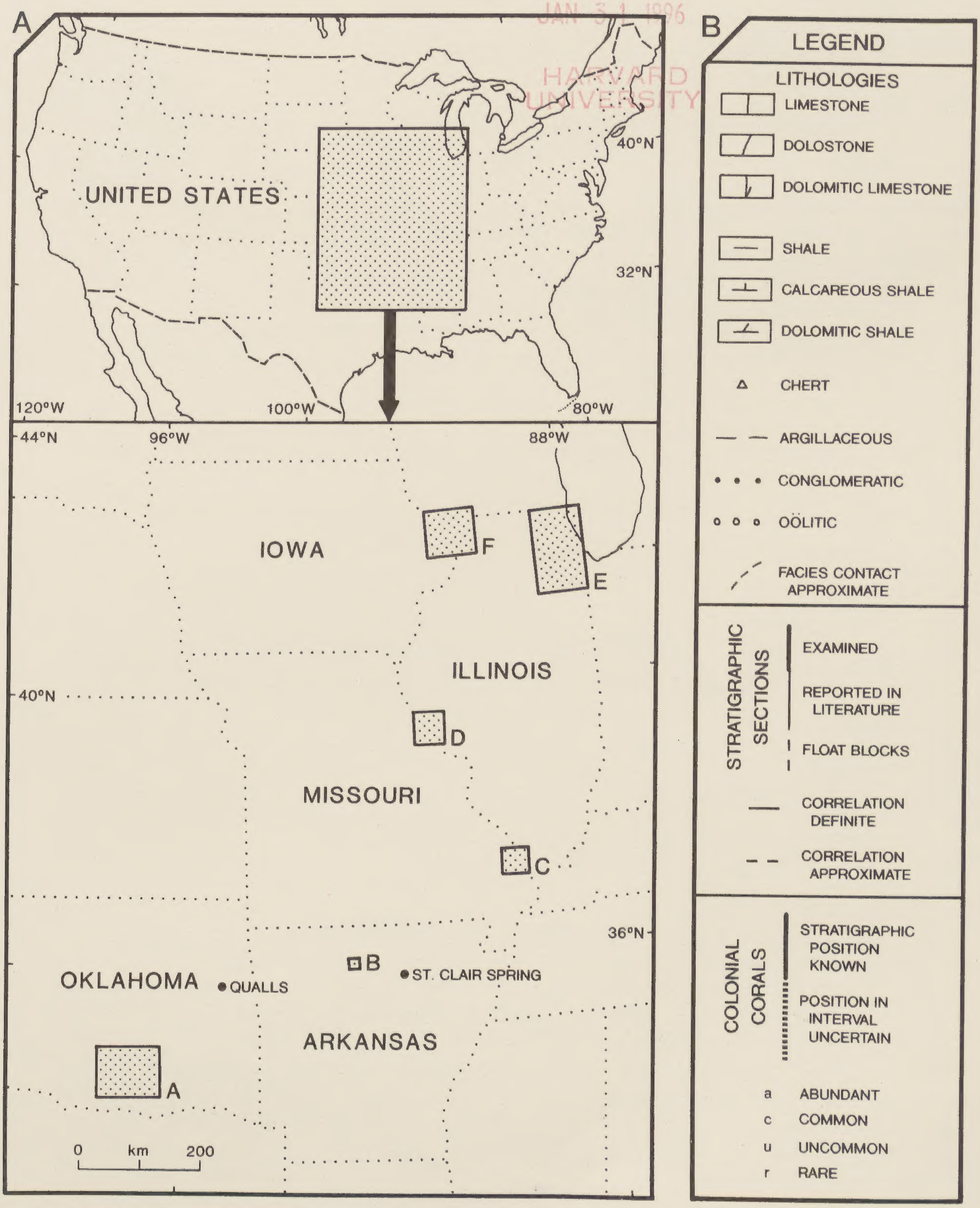
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Text-figure 1.—A, Index map showing study region in the east-central United States, and detail map showing outcrop areas (A–F) of uppermost Ordovician and lowermost Silurian strata containing colonial corals of the Edgewood Assemblage within the Edgewood Province, and other localities mentioned in text. A = south-central Oklahoma, B = western north-central Arkansas, C = southern Illinois and southeastern Missouri, D = west-central Illinois and northeastern Missouri, E = northeastern Illinois, F = northwestern Illinois and eastern Iowa. Details of areas A–F are shown in Text-figures 2–7. **B**, Legend of symbols for Text-figures 2–7.

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LATEST ORDOVICIAN TO EARLIEST SILURIAN COLONIAL CORALS OF THE EAST-CENTRAL UNITED STATES

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ABSTRACT

A distinctive assemblage of colonial corals occurs in uppermost Ordovician (Gamachian) to lowermost Silurian (lower Rhuddanian) strata within the east-central United States. This Edgewood Assemblage is strikingly different from Late Ordovician assemblages that preceded it in other parts of the North American cratonic interior, and differs from the Silurian assemblage that succeeded it. The Edgewood Assemblage existed during an important time of global environmental change and mass extinction. Some of the taxa have an Ordovician character; these include the youngest North American tetradiid, which is among the last representatives of an important Ordovician order. Other taxa represent first appearances of typically Silurian forms: the oldest definite plasmoporid, the earliest North American *Halysites,* and the first pycnostylid. Our study analyzes this significant assemblage in terms of biostratigraphy, biogeography, taphonomy, paleoecology, and intraspecific variability; the Silurian assemblage is also documented. With this information, we contribute to the knowledge of corals and the history of biological and physical events during this critical time interval, and to the solution of geologic problems such as the age, correlation, and depositional environment of stratigraphic units.

Colonial corals of the Edgewood Assemblage occur in Oklahoma, Arkansas, Missouri, and Illinois, occupying a region known as the Edgewood Province. We recognize the following new taxa: *Propora savagei* n. sp., *Halysites alexandricus* n. sp., and *Catenipora lawrencica* n. sp. Diversity in this province generally decreases northward, reflecting a gradient from the most open, normal-marine conditions nearest the paleocontinental margin, to increasing restriction farther into the interior. Detailed paleoenvironmental determinations are possible using comparative taphonomy and paleoecology. Proportions of abraded coralla and degrees of abrasion increase with energy level. Proportions of coralla in growth orientation are higher in lower energy environments; they also increase from columnar growth forms to bulbous and high domical forms to low domical forms, and with corallum size. Ratios of bulbous:domical forms and corallum height:width, and usually inferred growth rates, increase with sedimentation rate and decreasing substrate stability. Proportions of composite coralla increase with decreasing sediment cohesion and substrate stability. Large corallum sizes reflect prolonged environmental stability. In some cases, corals are active encrusters and substrates for encrusters; this indicates substrate availability and stability, low sedimentation rate, and low turbidity.

Two or perhaps three species of the Edgewood Assemblage occur outside the Edgewood Province. The strongest affinities of this assemblage are with latest Ordovician to earliest Silurian coral faunas of Anticosti Island, Québec. The Edgewood Assemblage is strikingly different from the slightly older, typical Late Ordovician faunas in the North American interior. The disappearance of these typical Ordovician assemblages was related to habitat loss during a major glacio-eustatic drop at the end of the Richmondian. In the Gamachian, minor transgressions into the southern–central portion of the Edgewood Province occurred as sea level fluctuated during the glacial maximum. Corals were introduced from the continental margin or were derived from forms previously restricted to the margin. Dispersion into the northern part of the province accompanied expansion of suitable habitat areas during the early phase of the major latest Gamachian–Rhuddanian transgression associated with deglaciation.

Colonial corals are uncommon in strata immediately above those containing the Edgewood Assemblage in the east-central United States. This Silurian assemblage, including *Paleofavosites adaensis* n. sp., appears in the upper Rhuddanian. The changeover from Edgewood to Silurian assemblages occurred as water depth and temperature were generally increasing during the Rhuddanian, but apparently coincided with a minor regressive event. We infer that as areas in the east-central United States became inhospitable, geographic ranges of Edgewood species were reduced. Most became extinct, but some underwent rapid evolution in small populations. The descendants dispersed and new immigrants arrived as suitable habitat areas expanded when the transgression resumed. Two Edgewood species survived briefly in a local refugium.

Comparisons of patterns of variation in different species indicate that inherent variabilities of different coral orders are not the same, and that certain types of variation tend to recur among species and among orders. Some of the general similarities and differences among taxa are linked principally to structural factors that controlled the ways in which colonial corals grew. Genotypic and ecophenotypic factors acted in concert with the structural control of growth to determine variation within individual species.

INTRODUCTION

The best known, most fossiliferous, and perhaps stratigraphically most complete Ordovician–Silurian boundary sections in the cratonic interior of North America occur in the east-central United States (see Bergström and Boucot, 1988; Text-fig. 1A, index map, foldout inside front cover). Upper Ordovician Richmondian beds were deposited in a vast epeiric sea and are mainly argillaceous. They are succeeded by uppermost Ordovician (Gamachian) to lowermost Silurian (lowermost Llandovery) units that are predominantly carbonate, typically thin, and of limited areal distribution. These in turn are overlain by carbonate strata of Llandovery age. The Gamachian beds represent a regressive phase corresponding to the latest Ordovician glacial maximum, but were probably deposited during minor transgressions as sea level fluctuated (see Amsden, 1986; McAuley and Elias, 1990). Lower Llandovery sediment accumulated during the major transgression associated with deglaciation. During Late Ordovician to Early Silurian time, North America was located on the equator, unattached to other paleocontinents (Scotese and McKerrow, 1990, figs. 9, 10). Continental glaciation in the latest Ordovician was centered on the African portion of Gondwana, in a south-polar position (Brenchley *et al.*, 1991, fig. 1).

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The biotas within these deposits in the east-central United States are of particular importance for several reasons. Stratigraphic and geographic distributions of various groups must be determined in order to establish a means for reliable age determination and correlation in regions where graptolites used to define the systemic boundary are absent (see Bergström and Boucot, 1988). The major mass extinction during latest Ordovician time may have been the second largest in the Phanerozoic (Sepkoski, 1986). This mass extinction and subsequent recovery in the Early Silurian have been related to global climatic, eustatic, and oceanographic changes (*e.g.*, Brenchley, 1989). In order to understand fully the patterns and processes of these bioevents, much remains to be learned at the species level in an accurate framework of time, environment, and biogeography. Data from cratonic interiors are essential because of the importance of "perched faunas" in the extensive epeiric seas that were characteristic of the Paleozoic (see Sheehan, 1988). Evolution and extinction in these faunal realms seem to have been related to the recurrent transgressions and regressions in cratonic areas. Faunal groups in the uppermost Ordovician to lowermost Silurian of the east-central United States that are best known are the brachiopods (*e.g.*, Amsden, 1974, 1986), conodonts (*e.g.*, Thompson and Satterfield, 1975; Barrick, 1986), and corals (see below).

The distinctive assemblage of solitary and colonial corals that occurs in Gamachian to lower Lower Llandovery (lower Rhuddanian) strata of the east-central United States has been termed the Edgewood Assemblage (see Elias and Young, 1992; Text-fig. 1A, detail map). The subclasses Rugosa Milne-Edwards and Haime and Tabulata Milne-Edwards and Haime are represented. The only coral known from the immediately underlying Richmondian beds in this region is *Salvadorea randi* (Elias), a solitary rugosan; it is not related to any Edgewood species. The Edgewood Assemblage is succeeded by an assemblage of Silurian rugose and tabulate corals in upper Lower Llandovery (upper Rhuddanian) strata. Our present comprehensive study of the Tabulata and colonial Rugosa in these deposits forms a companion to the work on solitary Rugosa by Elias (1982, 1992) and McAuley and Elias (1990). Together, these publications comprise the first thorough examination of an entire coral fauna from the latest Ordovician to earliest Silurian.

In this monograph we precisely document the full stratigraphic and geographic distribution of the Edgewood colonial corals, consider their biostratigraphic and biogeographic significance, and investigate their taphonomy, paleoecology, and intraspecific variability. Colonial corals of the succeeding Silurian assemblage in the study region are also documented because of their importance in delineating the stratigraphic limits of the Edgewood Assemblage and in interpreting the history of events, both biological and physical. With this information, we contribute to the knowledge of corals during this critical time interval, and to the solution of geologic problems such as the age, correlation, and depositional environment of units and the effects and timing of sea-level changes. Syntheses based on the entire solitary and colonial coral fauna in uppermost Ordovician to lowermost Silurian strata of the east-central United States have been and will be presented elsewhere (*e.g.*, Elias and Young, 1992).

Strata containing corals of the Edgewood Assemblage are exposed in six outcrop areas (Text-fig. 1A, detail map, foldout inside front cover). The region of the east-central United States in which this particular assemblage occurs has been named the Edgewood Province (Elias, 1982). We selected 32 stratigraphic sections for examination in this study. They provide representative geographic coverage of the interval containing Edgewood corals, as well as some exposure of the immediately underlying and overlying beds. All sections have been described in previous literature, and fossils have been listed from most (see *Appendix*, pp. 104–106). Each stratigraphic section, as well as a bulk rock sample provided by W. W. Craig from the section in north-central Arkansas, was thoroughly examined for colonial coralla. All specimens seen were collected; they were found at 24 sections. Additional material from some of these, as well as other sections, was incorporated into our study from collections made by R. J. Elias and R. J. McAuley in Oklahoma and southeastern Missouri, by A. F. Foerste in southern Illinois, by T. E. Savage in southern and northeastern Illinois and northeastern Missouri, and by H. F. Crooks in northeastern Illinois.

A total of 324 colonial coralla of the Edgewood Assemblage and 37 from the Silurian assemblage are identified to the species level and documented here. Their abundance within collection intervals in the stratigraphic sections we studied was estimated qualitatively, taking into account the absolute number of specimens, thickness and lateral extent of the interval, and quality of the exposure. Ranges in number of coralla for each abundance category are as follows: rare, 1–2; uncommon, 2–6; common, 4–19; and abundant, 11–50.

Colonial coralla from elsewhere in North America were examined for comparative purposes as necessary. We studied one specimen from the Hudson Bay Lowland of Manitoba, six from southern Ontario, six from the Gaspé Peninsula of Québec, and ten from Anticosti Island, Québec.

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DISTRIBUTION OF COLONIAL CORALS

INTRODUCTION

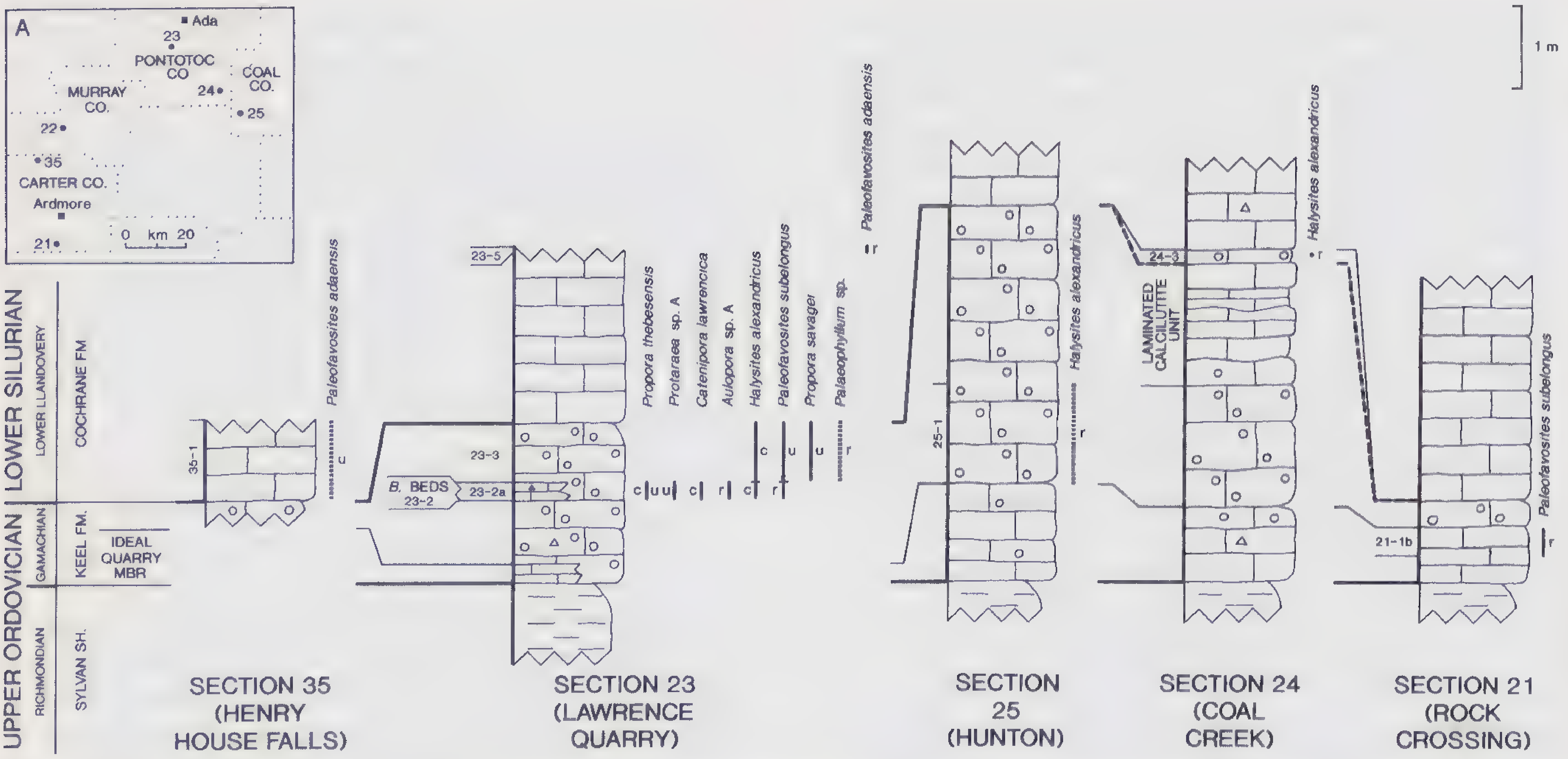
Uppermost Ordovician to lowermost Silurian deposits containing corals of the Edgewood Assemblage occur in six outcrop areas in the east-central United States (Text-fig. 1A, foldout inside front cover). McAuley and Elias (1990, pp. 9–23) discussed the lithostratigraphy, biota, age, and paleoenvironment for each area (see also Elias, 1992). The history of study and the distribution of colonial corals in these areas are documented below.

SOUTH-CENTRAL OKLAHOMA

Uppermost Ordovician to lowermost Silurian stratigraphy in this area is shown in Text-figure 2. Corals are not known to occur in the Sylvan Shale. Colonial corals identified as *Lyellia thebesensis* Foerste and *Halysites catenularia* (Linnaeus) were listed from the Ideal Quarry Member of the Keel Formation by Maxwell (1936, p. 49, table 1; unit referred to as Hawkins Limestone therein). The following have been reported previously from oölites of the Keel Formation: *Favosites niagarensis* Hall (Reeds, 1911, p. 259; upper oölitic zone, oölitic member, Chimneyhill Limestone therein); *L. thebesensis, H. catenularia, Favosites favosus* (Goldfuss), and *Favosites* sp. (Maxwell, 1936, table 2); and *Halysites* sp. (Amsden, 1957, p. 15; 1960, p. 44).

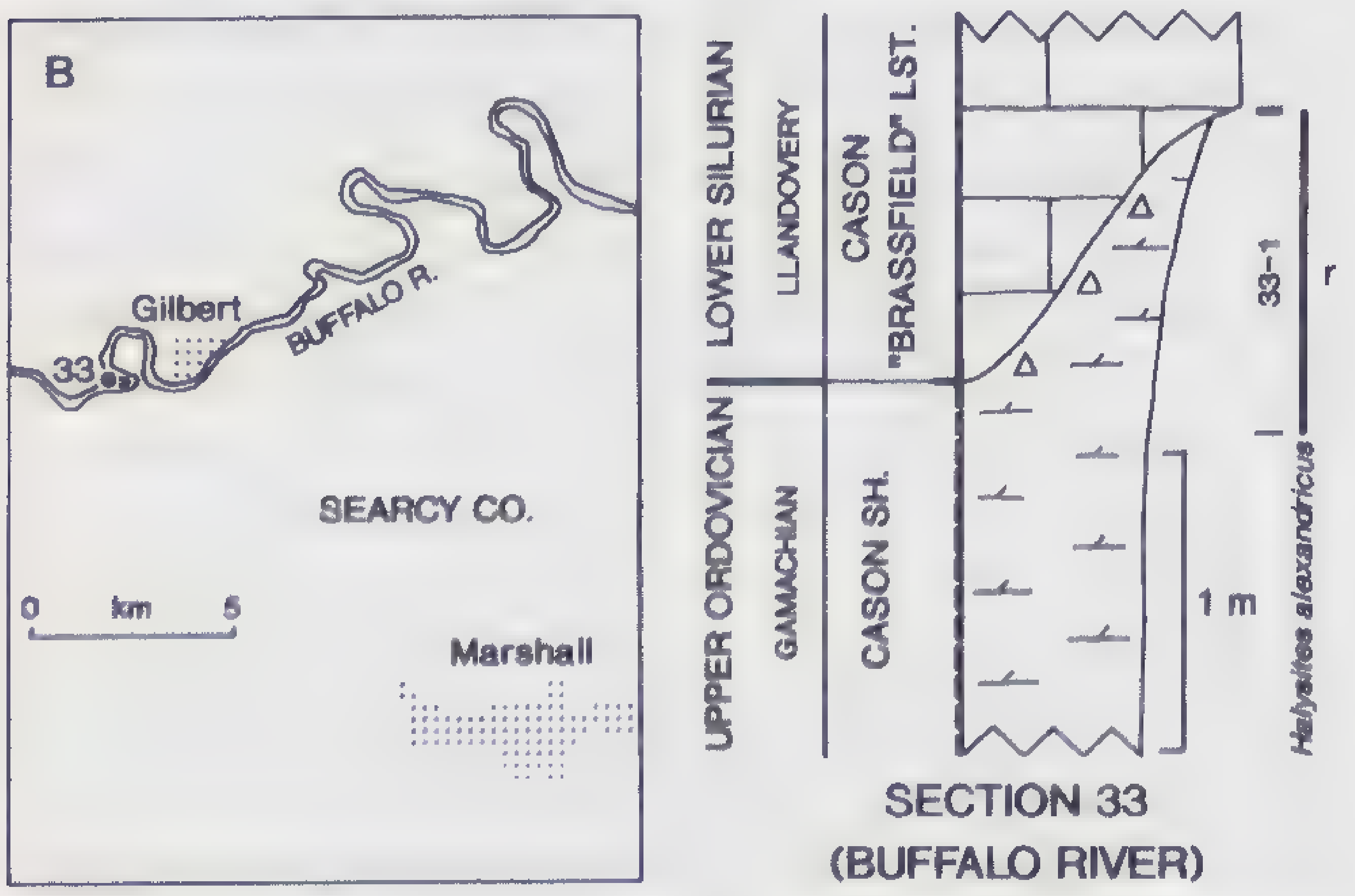
Paleofavosites subelongus (Savage) was the only species recovered from the Ideal Quarry Member of the Keel Formation during the present study. We found the following in the *Brevilamnulella* beds of the Keel: *Propora thebesensis* (Foerste), *Protaraea* sp. A, *Halysites alexandricus* n. sp., *Catenipora lawrencica* n. sp., *P. subelongus,* and *Aulopora* sp. A. The colonial rugose corals that McAuley and Elias (1990, p. 8) reported seeing in the *Brevilamnulella* beds may have been coralla of *P. subelongus* with prominent septal spines. From oölites in the lower Keel Formation (Section-intervals 23-2a, 23-3, 25-1), we obtained *P. thebesensis, Propora savagei* n. sp., *H. alexandricus, P. subelongus,* and *Palaeophyllum* sp. The only colonial coral we discovered in an oölite of the upper Keel (Section-interval 24-3) is *H. alexandricus.* Coralla were not observed in the Keel at Section 22 (Cedar Village).

From the Cochrane Formation, *Favosites favosus* was listed by Reeds (1911, table 2; glauconitic member, Chimneyhill Limestone therein), and that species as well as *Halysites catenularia* were identified by Maxwell (1936, p. 59, table 3). In the lower Cochrane, we found only *Paleofavosites adaensis* n. sp. The distribution of corals in the Keel and Cochrane formations, based on collections made during the present study, is shown in Text-figure 2.


A
Ada
23
PONTOTOC CO
COAL CO.
MURRAY CO.
24
25
22
35
CARTER CO.
Ardmore
0 km 20
21
UPPER ORDOVICIAN
LOWER SILURIAN
RICHMONDIAN
GAMACHIAN
LOWER LLANDOVERY
SYLVAN SH.
KEEL FM.
IDEAL QUARRY MBR
COCHRANE FM.
35-1
Paleofavosites adaensis
23-5
23-3
B. BEDS 23-2
23-2a
Propora thebesensis
Protaraea sp. A
Catenipora lawrencica
Aulopora sp. A
Halysites alexandricus
Paleofavosites subelongus
Propora savagei
Palaeophyllum sp.
25-1
Halysites alexandricus
LAMINATED CALCILUTITE UNIT
24-3
21-1b
1 m
SECTION 35 (HENRY HOUSE FALLS)
SECTION 23 (LAWRENCE QUARRY)
SECTION 25 (HUNTON)
SECTION 24 (COAL CREEK)
SECTION 21 (ROCK CROSSING)

Text-figure 2.—Locality map (A) and stratigraphic sections (to scale) in south-central Oklahoma (see Text-fig. 1A, foldout inside front cover). For legend, see Text-figure 1B. *B.* = *Brevilamnulella.* Occurrences of species in *Brevilamnulella* beds (Section-interval 23-2) and in oölite lateral to *Brevilamnulella* beds (Section-interval 23-2a) are indicated by abundance symbols on left and right sides, respectively, of range lines beside those intervals. For references and precise locations of sections, see *Appendix* (p. 104).

The Pettit Formation is a thin oölitic unit that occurs locally in northeastern Oklahoma (Amsden, 1980, pp. 23, 24). Identifiable fossils have not been recovered from this formation, and correlation with the Keel Formation is tentative. Colonial coralla were not found in our examination of a bulk rock sample from the Pettit at section Ch4 of Amsden and Rowland (1965, pp. 24, 95, 96, fig. 7, pl. B), located about 100 m north of the type section near Qualls (see Text-fig. 1A, detail map, foldout inside front cover).


B
Gilbert
33
BUFFALO R.
SEARCY CO.
0 km 5
Marshall
UPPER ORDOVICIAN
LOWER SILURIAN
GAMACHIAN
LLANDOVERY
CASON SH.
CASON "BRASSFIELD" LST.
33-1
1 m
Halysites alexandricus
SECTION 33 (BUFFALO RIVER)

Text-figure 3.—Locality map (B) and stratigraphic section in western north-central Arkansas (see Text-fig. 1A, foldout inside front cover). For legend, see Text-figure 1B. For references and precise location of section, see *Appendix* (p. 104).

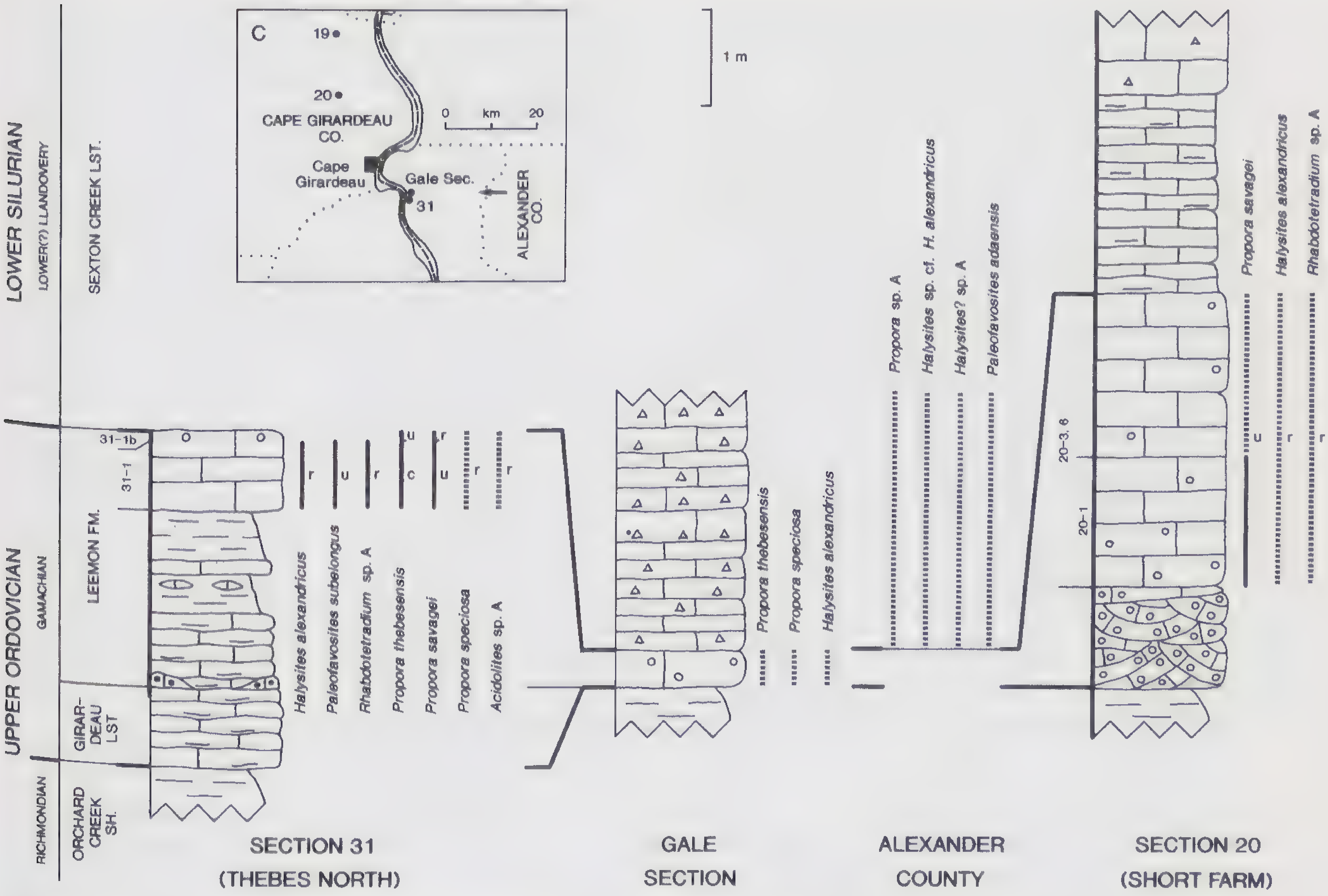
WESTERN NORTH-CENTRAL ARKANSAS

Lemastus (1979, pp. 42, 88) noted the presence of silicified corals in uppermost layers of the Cason Shale at Section 33 (Buffalo River). McAuley and Elias (1990, p. 10) reported a halysitid from those strata. The latter corallum, which we identify as *Halysites alexandricus,* occurs in chert that represents a silicified oölite (Text-fig. 3). We did not observe corals in the Cason "Brassfield" Limestone above the Cason Shale at Section 33. Maher and Lantz (1952, pp. 5, 6) reported unidentifiable solitary corals, but no colonial forms, from the "Brassfield" at a locality about 3 km to the east.

The Cason Shale at Section 33 (Buffalo River) has been correlated with the Cason Oölite at St. Clair Spring in eastern north-central Arkansas (see McAuley and Elias, 1990, pp. 9, 10, 55, fig. 3; Text-fig. 1A, detail map, foldout inside front cover). We did not find colonial coralla in the oölitic unit at that locality.

SOUTHERN ILLINOIS AND SOUTHEASTERN MISSOURI

Uppermost Ordovician to lowermost Silurian stratigraphy in this area is shown in Text-figure 4. Corals are not known to occur in the Girardeau Limestone, and colonial forms are not known from the Orchard Creek Shale. The following colonial corals have been identified previously from the Leemon Formation at or near Section 31 (Thebes North): undetermined *Heliolites* Dana (Worthen, 1866, p. 127; unit referred to


LOWER SILURIAN
LOWER(?) LLANDOVERY
SEXTON CREEK LST.
UPPER ORDOVICIAN
GAMACHIAN
LEEMON FM.
GIRARDEAU LST
RICHMONDIAN
ORCHARD CREEK SH.
C
19
20
CAPE GIRARDEAU CO.
Cape Girardeau
Gale Sec.
31
0 km 20
ALEXANDER CO.
1 m
31-1b
31-1
Halysites alexandricus
Paleofavosites subelongus
Rhabdotetradium sp. A
Propora thebesensis
Propora savagei
Propora speciosa
Acidolites sp. A
r
u
c
Propora thebesensis
Propora speciosa
Halysites alexandricus
Propora sp. A
Halysites sp. cf. H. alexandricus
Halysites? sp. A
Paleofavosites adaensis
20-3.6
20-1
Propora savagei
Halysites alexandricus
Rhabdotetradium sp. A
SECTION 31 (THEBES NORTH)
GALE SECTION
ALEXANDER COUNTY
SECTION 20 (SHORT FARM)

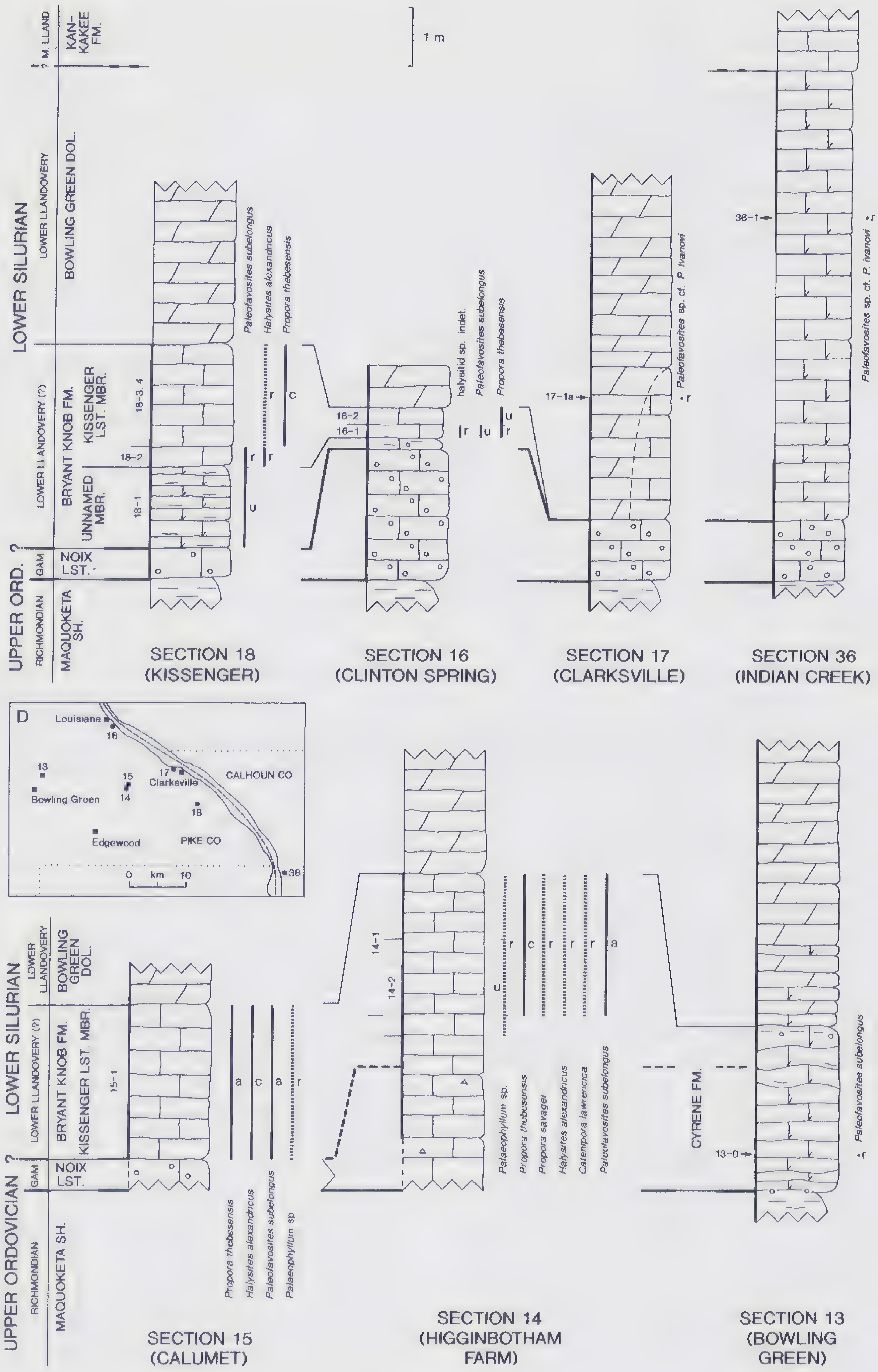
Text-figure 4.—Locality map (C) and stratigraphic sections (to scale) in southern Illinois and southeastern Missouri (see Text-fig. 1A, foldout inside front cover). For legend, see Text-figure 1B. For references and precise locations of sections, see *Appendix* (p. 104); for information on Sexton Creek corals in Alexander County, see text.

as lowermost Clear Creek Limestone therein); *Lyellia thebesensis* (Foerste, 1909, p. 95); and *L. thebesensis, Calvinia edgewoodensis* Savage, *Favosites subelongus* Savage, and *Calapoecia favositoidea* Savage (Savage, 1913, pp. 20, 24; 1917, pp. 78, 82; Edgewood Formation therein). *Lyellia thebesensis* and *C. edgewoodensis* have been reported from the Leemon at the Gale Section (Savage, 1913, p. 21; 1917, p. 79; Edgewood Formation therein). They were referred to as *Plasmopora thebesensis* (Foerste) and *Heliolites? edgewoodensis* in Savage (1910, p. 333).

Based on studies of our own collections as well as those of Foerste and of Savage, we recognize the following species in the Leemon Formation: *Propora thebesensis, Propora savagei, Propora speciosa* (Billings), *Acidolites* sp. A, *Halysites alexandricus, Paleofavosites subelongus,* and *Rhabdotetradium* sp. A. *Calvinia edgewoodensis* is a synonym of *P. speciosa* (see *Discussion,* pp. 60, 61), and *Calapoecia favositoidea* is a synonym of *P. subelongus* (see *Discussion,* p. 87). The distribution of these corals is shown in Text-figure 4. We did not find colonial coralla in the Leemon at Section 19 (New Wells).

Favosites favosus and *Halysites catenulatus* [*sic*] (Linnaeus) were identified previously from the Sexton Creek Limestone at a locality 5.8 km south of Section 31 (Thebes North) (Savage, 1913, p. 16; 1917, p. 74). We recognize the following colonial corals in Savage's collections from that unit in Alexander County, Illinois: *Propora* sp. A, *Halysites* sp. cf. *H. alexandricus, Halysites*? sp. A, and *Paleofavosites adaensis* (Text-fig. 4). Specimens were not found during our examination of the lower Sexton Creek at Section 19 (New Wells) or Section 20 (Short Farm).

Birkhead (1967, p. 28) reported *Halysites* sp., *Heliolites* sp., and *Lyellia* sp. from two localities in Cape Girardeau County, Missouri. The strata were assigned to the Sexton Creek Formation at one locality and to the Cyrene Member of the Edgewood Formation at the other. His photograph of the latter locality, showing irregular beds of chert (Birkhead, 1967, fig. 5), suggests that it is also Sexton Creek Limestone. Illustrations of


LOWER SILURIAN
? M. LLAND
KAN-KAKEE FM.
LOWER LLANDOVERY
BOWLING GREEN DOL.
LOWER LLANDOVERY (?)
BRYANT KNOB FM.
KISSENGER LST. MBR.
UNNAMED MBR.
UPPER ORD. ?
GAM
NOIX LST.
RICHMONDIAN
MAQUOKETA SH.
1 m
18-3, 4
18-2
18-1
Paleofavosites subelongus
Halysites alexandricus
Propora thebesensis
r
r
u
r
c
16-2
16-1
halysitid sp. indet.
Paleofavosites subelongus
Propora thebesensis
r
u
r
u
r
17-1a
Paleofavosites sp. cf. P. ivanovi
r
36-1
Paleofavosites sp. cf. P. ivanovi
r
SECTION 18 (KISSENGER)
SECTION 16 (CLINTON SPRING)
SECTION 17 (CLARKSVILLE)
SECTION 36 (INDIAN CREEK)
D
Louisiana
16
13
15
14
17
Clarksville
CALHOUN CO
Bowling Green
18
Edgewood
PIKE CO
0 km 10
36
LOWER SILURIAN
LOWER LLANDOVERY
BOWLING GREEN DOL.
LOWER LLANDOVERY (?)
BRYANT KNOB FM.
KISSENGER LST. MBR.
15-1
UPPER ORDOVICIAN ?
GAM
NOIX LST.
RICHMONDIAN
MAQUOKETA SH.
a
c
a
r
Propora thebesensis
Halysites alexandricus
Paleofavosites subelongus
Palaeophyllum sp
14-1
14-2
u
r
c
r
r
r
a
Palaeophyllum sp.
Propora thebesensis
Propora savagei
Halysites alexandricus
Catenipora lawrencica
Paleofavosites subelongus
CYRENE FM.
13-0
Paleofavosites subelongus
r
SECTION 15 (CALUMET)
SECTION 14 (HIGGINBOTHAM FARM)
SECTION 13 (BOWLING GREEN)

coralla from that locality, identified by Birkhead as *Lyellia* sp. (Birkhead, 1967, pl. 4, figs. 4a, 4b) and *Heliolites* sp. (Birkhead, 1967, pl. 4, figs. 5a, 5b), show a probable *Propora* Milne-Edwards and Haime and a questionable representative of the family Coccoseridae Kiaer, respectively. The specimens have not been located (Carter, oral commun., 1992).

WEST-CENTRAL ILLINOIS AND NORTHEASTERN MISSOURI

Uppermost Ordovician to lowermost Silurian stratigraphy in this area is shown in Text-figure 5. Corals are not known from the Maquoketa Shale in west-central Illinois and northeastern Missouri. The following colonial (or possibly colonial) corals have been identified previously from strata that represent the combined Noix Limestone and Bryant Knob Formation in northeastern Missouri: *Acervularia Davidsoni?* [*sic*] Milne-Edwards and Haime (Swallow, 1855, p. 107; unit referred to as Oölitic Limestone therein); *Halysites catenulata* [*sic*] (Linnaeus), *Favosites* sp? [*sic*], and *Cyathophyllum* sp? [*sic*] (Rowley, 1908, p. 23; oölitic limestone therein); and *Lyellia thebesensis, Halysites catenulatus* [*sic*], *Favosites subelongus,* and *Calapoecia favositoidea* (Savage, 1913, p. 24; 1917, p. 82; Noix Oölite therein). *Halysites* Fischer von Waldheim has been noted in blocks considered to be from the Noix Limestone (Amsden, 1974, fig. 9). The following have been identified from strata that represent the combined Cyrene Formation and Bowling Green Dolomite in northeastern Missouri: *Lyellia?* sp? [*sic*], *H. catenulata, Favosites* sp? [*sic*], *Columnaria* sp? [*sic*], and *Cyathophyllum* sp? [*sic*] (Rowley, 1908, p. 23; brown, earthy limestone therein); and *L. thebesensis, F. subelongus,* and *C. favositoidea* (Savage, 1913, p. 24; 1917, p. 82; Edgewood Formation therein). *Lyellia thebensis* [*sic*] (Foerste) was listed from the Bowling Green in west-central Illinois by Rubey (1952, p. 170).

Our understanding of colonial corals and their distribution in this area is based on collections made during the present study (Text-fig. 5), and on our examination of material collected by T. E. Savage (University of Illinois at Urbana–Champaign collection). We have not found colonial coralla in the Noix Limestone. *Paleofavosites subelongus* is the only species known from the unnamed member of the Bryant Knob Formation. The following are present in the Kissenger Limestone Member of the Bryant Knob: *Propora thebesensis, Propora savagei, Halysites alexandricus, Catenipora lawrencica, P. subelongus,* and *Palaeophyllum* sp. *Calapoecia favositoidea* is a synonym of *P. subelongus* (see *Discussion,* p. 87). We obtained *P. subelongus* from the Cyrene Formation at Section 13 (Bowling Green). The only colonial coral known from the Bowling Green Dolomite is *Paleofavosites* sp. cf. *P. ivanovi* Sokolov.

In Savage's collections made near Edgewood, Missouri (see Text-fig. 5, locality map), we identify the colonial corals *Propora thebesensis, Propora savagei, Plasmopora* sp. cf. *P. logani* Young and Noble, and *Paleofavosites subelongus.* All are considered to be from the Cyrene Formation, and not from the Bowling Green Dolomite. This is based on statements by Savage (1913, pp. 22, 64, 65; 1917, pp. 80, 114, 115), on the lithology of matrix adhering to one specimen, on the absence of these species in known Bowling Green beds, on the presence of *P. subelongus* in known Cyrene strata, and on the occurrence of *P. thebesensis, P. savagei,* and *P. subelongus* in the Bryant Knob Formation, which together with the Noix Limestone is a lateral equivalent of the Cyrene (see McAuley and Elias, 1990, p. 15).

NORTHEASTERN ILLINOIS

Uppermost Ordovician to lowermost Silurian stratigraphy in this area is shown in Text-figure 6. Corals are not known from the Maquoketa Group in northeastern Illinois. The following colonial corals have been identified previously from the Wilhelmi Formation at Section 37 (Essex): *Halysites catenulatus* [*sic*] and *Favosites* cf. *niagarensis* (Savage, 1912, p. 100; 1913, p. 29; 1917, p. 87; unit referred to as Essex Limestone therein); and *Lyellia* cf. *thebesensis* and *F. niagarensis* (Athy, 1928, p. 40; Essex Limestone therein). From loose blocks of the Wilhelmi at that section, we recovered *Halysites alexandricus, Paleofavosites subelongus,* and *Aulopora* sp. A. One poorly preserved favositid corallum, referred to as *Paleofavosites* sp. indet., was found in the upper portion of the Schweizer Member of the Wilhelmi Formation at Section 4 (Schweizer West).

Savage (1914, p. 31) identified *Lyellia thebesensis* from 3.2 km and 5.6 km south of Channahon, Illinois (see Text-fig. 6, locality map). We have studied his collections from the former locality, and recognize *Pro-*

←

Text-figure 5.—Locality map (D) and stratigraphic sections (to scale) in west-central Illinois and northeastern Missouri (see Text-fig. 1A, foldout inside front cover). For legend, see Text-figure 1B. Gam. = Gamachian. Abundance symbols on left and right sides of range line for *Palaeophyllum* sp. at Section 14 (Higginbotham Farm) refer to Section-intervals 14-2 and 14-1, respectively. For references and precise locations of sections, see *Appendix* (pp. 104, 105).

pora thebesensis, Halysites alexandricus, and *Paleofavosites subelongus.* They are considered to be from the Wilhelmi Formation. The matrix of one specimen contains a corallum of the solitary rugosan *Streptelasma subregulare* (Savage), which is restricted to the Wilhelmi in this area (see McAuley and Elias, 1990, p. 20, fig. 7).

From the Elwood Formation, we recovered *Propora* sp. aff. *P. affinis* (Billings) and *Paleofavosites* sp. A. The distribution of colonial corals found in the Wilhelmi and Elwood formations during the present study is shown in Text-figure 6. We did not observe colonial coralla in the Wilhelmi at Section 3 (Garden Prairie), or in the Wilhelmi and lower Elwood at Section 34 (Belvidere South).

NORTHWESTERN ILLINOIS AND EASTERN IOWA

Uppermost Ordovician to lowermost Silurian stratigraphy in this area is shown in Text-figure 7. Colonial corals are not known from the Brainard Shale in northwestern Illinois and eastern Iowa. In the Mosalem Formation at Section 32 (Thomson East), *Pycnostylus*? sp. was previously identified from the fill of small, local channels (McAuley and Elias, 1990, p. 22, fig. 9; Section-interval 32-1b). We document it as *Pycnostylus* sp. A. The presence of tabulate corals in a bed on the old quarry floor was reported by McAuley and Elias (1990, p. 22; Section-interval 32-1z). We obtained *Propora thebesensis, Halysites alexandricus,* and *Paleofavosites subelongus* from that coral-rich bedding surface, which appears to be at about the same stratigraphic position as the top of the channels. *Propora thebesensis, Propora speciosa,* and *Paleofavosites* sp. cf. *P. subelongus* were found in the upper Mosalem, above the filled channels (Section-interval 32-1c). At Section 10 (Lost Mound), *Paleofavosites adaensis* occurs near the top of the Mosalem. The distribution of these corals is shown in Text-figure 7.

We found poorly preserved specimens, identified as favositid sp. indet., 3.3 m below the top of the Mosalem Formation at both Section 8 (King) and Section 30 (Thomson Northeast). Colonial coralla were not observed in the Mosalem at Section 9 (Winston), Section 11 (Schapville), Section 12 (Stockton), or Section 26 (Bellevue).

COLONIAL CORAL ASSEMBLAGES

The stratigraphic and geographic distribution of colonial corals in uppermost Ordovician to lowermost Silurian sequences within the east-central United States is summarized in Text-figure 8 (foldout inside back cover). We recognize two assemblages. The Edgewood Assemblage (Table 1) includes colonial corals representing 13 species and 11 genera. Tabulates of five orders account for over 95% of specimens; the remainder are colonial rugosans of a single order. A total of 84% of specimens belong to the following three species: *Paleofavosites subelongus, Propora thebesensis,* and *Halysites alexandricus.* In addition to being numerically dominant, these species are also the most widely distributed; *H. alexandricus* occurs in all six outcrop areas. Stratigraphically, the Edgewood Assemblage is situated above Upper Ordovician Richmondian beds that are not known to contain colonial corals in the study region.

The Edgewood Assemblage is succeeded by a Silurian assemblage that includes tabulates belonging to *Propora, Halysites,* and *Paleofavosites* Twenhofel (Table 2). Although these genera are represented in both the Silurian and Edgewood assemblages, the characteristic species are different. *Paleofavosites adaensis* is the most widely distributed Silurian form, occurring in south-central Oklahoma as well as southern and northwestern Illinois. *Halysites* sp. cf. *H. alexandricus* and *Paleofavosites* sp. cf. *P. subelongus* of the Silurian assemblage are comparable to Edgewood taxa. Colonial corals of the Edgewood and Silurian assemblages are known to co-occur at only one locality, Section 32 (Thomson East) (see Text-fig. 7). There, *Propora thebesensis* and *Propora speciosa* are found with *Paleofavosites* sp. cf. *P. subelongus* in the upper Mosalem Formation. *Paleofavosites adaensis,* which is characteristic of the Silurian assemblage, is present in the upper Mosalem at Section 10 (Lost Mound).

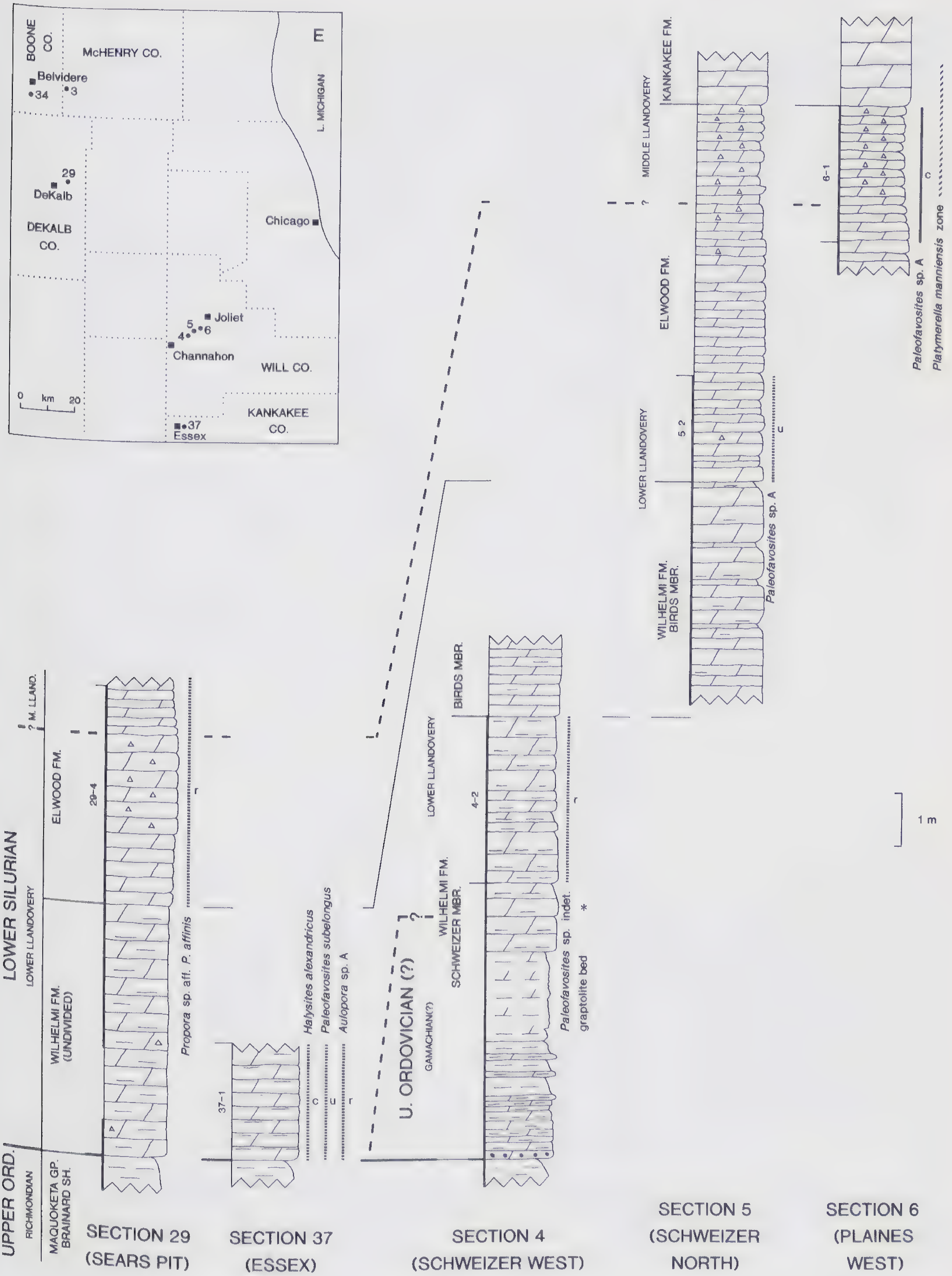
It is noteworthy that solitary rugose corals of the Silurian assemblage represent different genera from those in the Edgewood Assemblage (McAuley and Elias, 1990, table 1). Rugosan species of the two assemblages are not known to co-occur (Elias, 1992, p. 120).

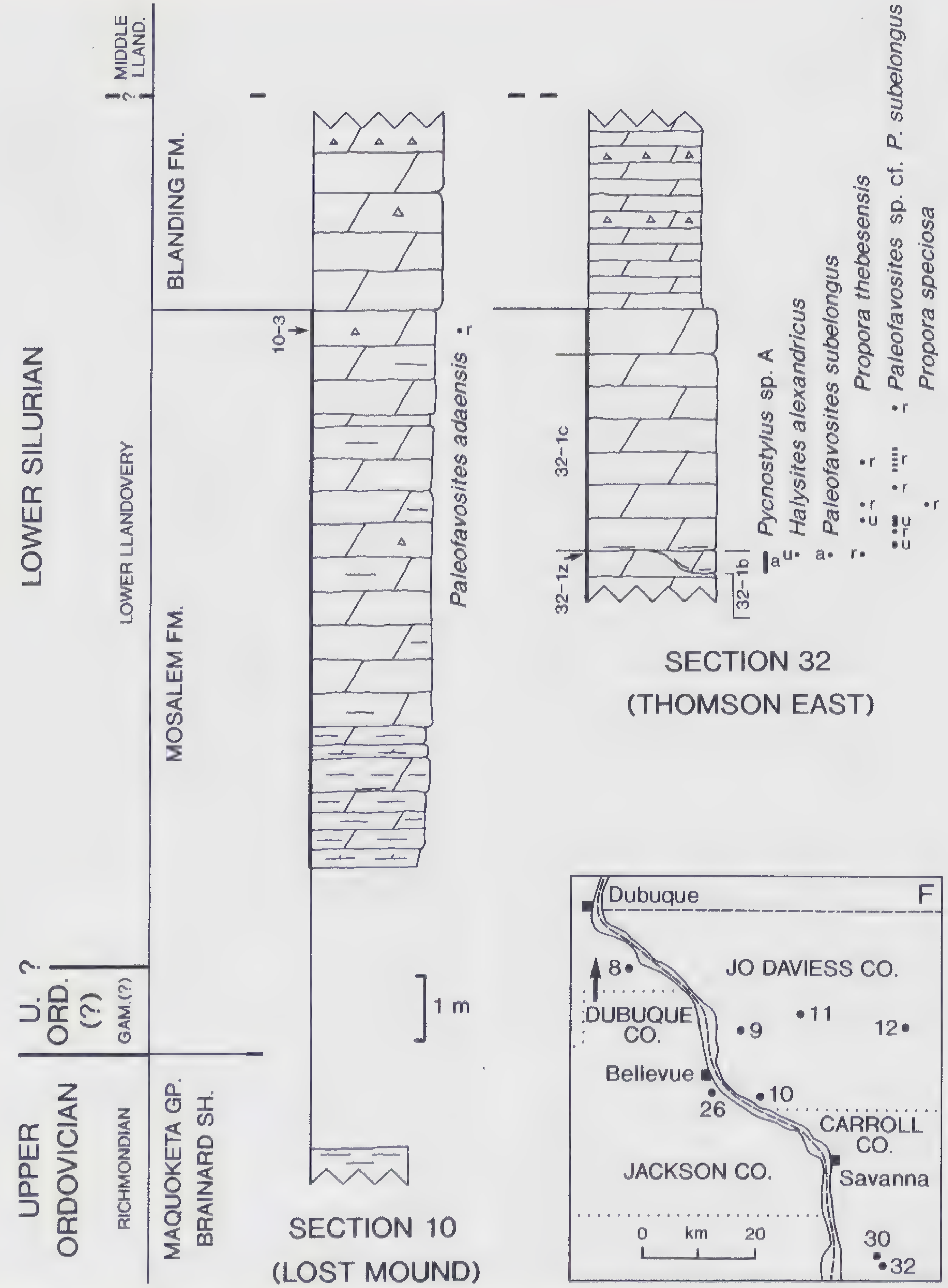
AGE OF UNITS AND REGIONAL CORRELATION

The age and correlation of uppermost Ordovician to lowermost Silurian strata in the east-central United States are summarized in Text-figure 8 (foldout inside back cover). The evidence, based on brachiopods, conodonts, corals, graptolites, lithology, stratigraphic position, and sea-level curves, has been discussed in detail by McAuley and Elias (1990), Elias and Young

→

Text-figure 6.—Locality map (E) and stratigraphic sections (to scale) in northeastern Illinois (see Text-fig. 1A, foldout inside front cover). For legend, see Text-figure 1B. For references and precise locations of sections, see *Appendix* (p. 105).


BOONE CO.
McHENRY CO.
Belvidere
34
3
L. MICHIGAN
E
29
DeKalb
DEKALB CO.
Chicago
Joliet
5
4
6
Channahon
WILL CO.
0 km 20
37
Essex
KANKAKEE CO.
LOWER SILURIAN
UPPER ORD.
RICHMONDIAN
MAQUOKETA GP. BRAINARD SH.
LOWER LLANDOVERY
WILHELMI FM. (UNDIVIDED)
ELWOOD FM.
? M. LLAND.
29-4
Propora sp. aff. P. affinis
r
37-1
Halysites alexandricus
Paleofavosites subelongus
Aulopora sp. A
c
u
r
U. ORDOVICIAN (?)
GAMACHIAN(?)
WILHELMI FM. SCHWEIZER MBR.
LOWER LLANDOVERY
BIRDS MBR.
4-2
Paleofavosites sp. indet.
graptolite bed
*
WILHELMI FM. BIRDS MBR.
LOWER LLANDOVERY
5-2
Paleofavosites sp. A
c
ELWOOD FM.
MIDDLE LLANDOVERY
?
KANKAKEE FM.
6-1
Paleofavosites sp. A
Platymerella manniensis zone
c
1 m
SECTION 29 (SEARS PIT)
SECTION 37 (ESSEX)
SECTION 4 (SCHWEIZER WEST)
SECTION 5 (SCHWEIZER NORTH)
SECTION 6 (PLAINES WEST)


LOWER SILURIAN
LOWER LLANDOVERY
MIDDLE LLAND.
?
BLANDING FM.
MOSALEM FM.
U. ORD. (?)
?
GAM.(?)
UPPER ORDOVICIAN
RICHMONDIAN
MAQUOKETA GP. BRAINARD SH.
10-3
Paleofavosites adaensis
r
1 m
SECTION 10 (LOST MOUND)
32-1c
32-1z
32-1b
Pycnostylus sp. A
Halysites alexandricus
Paleofavosites subelongus
Propora thebesensis
Paleofavosites sp. cf. P. subelongus
Propora speciosa
a
u
r
c
SECTION 32 (THOMSON EAST)
F
Dubuque
JO DAVIESS CO.
DUBUQUE CO.
Bellevue
CARROLL CO.
JACKSON CO.
Savanna
8
9
10
11
12
26
30
32
0 km 20

Text-figure 7.—Locality map (F) and stratigraphic sections (to scale) in northwestern Illinois and eastern Iowa (see Text-fig. 1A, foldout inside front cover). For legend, see Text-figure 1B. Gam. = Gamachian. Occurrences of species in Section-interval 32-1z are indicated by abundance symbols on left sides of range lines beside that interval. For references and precise locations of sections, see *Appendix* (pp. 105, 106).

Table 1.—Colonial corals of the Edgewood Assemblage, relative abundance based on all identified specimens (n = 324), and distribution in outcrop areas within the east-central United States. Specimens are individual coralla except for two of the three specimens of *Aulopora* sp. A, which appear to include several coralla, and the eight specimens of *Pycnostylus* sp. A, each of which includes several dissociated corallites. *A* = south-central Oklahoma, *B* = western north-central Arkansas, *C* = southern Illinois and southeastern Missouri, *D* = west-central Illinois and northeastern Missouri, *E* = northeastern Illinois, *F* = northwestern Illinois and eastern Iowa (see Text-fig. 1A, foldout inside front cover); × indicates an occurrence.

taxa	*relative abundance*	*distribution*					
		A	*B*	*C*	*D*	*E*	*F*
Subclass Tabulata	95.6%						
Order Heliolitida	33.5%						
Family Proporidae							
Propora thebesensis	25.9%	×	—	×	×	×	×
Propora savagei	4.9%	×	—	×	×	—	—
Propora speciosa	1.2%	—	—	×	—	—	—
Family Plasmoporidae							
Plasmopora sp. cf. *P. logani*	0.3%	—	—	—	×	—	—
Family Coccoserididae							
Acidolites sp. A	0.3%	—	—	×	—	—	—
Protaraea sp. A	0.9%	×	—	—	—	—	—
Order Halysitida	15.5%						
Family Halysitidae							
Halysites alexandricus	13.3%	×	×	×	×	×	×
Catenipora lawrencica	2.2%	×	—	—	×	—	—
Order Favositida	44.8%						
Suborder Favositina							
Superfamily Favositicae							
Family Favositidae							
Subfamily Favositinae							
Paleofavosites subelongus	44.8%	×	—	×	×	×	×
Order Auloporida	0.9%						
Superfamily Auloporicae							
Family Auloporidae							
Aulopora sp. A	0.9%	×	—	—	—	×	—
Order Tetradiida	0.9%						
Family Tetradiidae							
Rhabdotetradium sp. A	0.9%	—	—	×	—	—	—
Subclass Rugosa	4.4%						
Order Stauriida	4.4%						
Suborder Stauriina							
Family Stauriidae							
Palaeophyllum sp.	1.9%	×	—	—	×	—	—
Family Pycnostylidae							
Pycnostylus sp. A	2.5%	—	—	—	—	—	×

(1992), and Elias (1992). Here, we consider the biostratigraphic significance of colonial corals in the Edgewood and Silurian assemblages.

Two of the Edgewood proporids are known to occur outside the east-central United States. *Propora thebesensis* is present in the Ellis Bay Formation (uppermost Ordovician, Gamachian, to possibly lowermost Silurian, Lower Llandovery, lowermost Rhuddanian) and in the overlying Becscie Formation (Rhuddanian) on Anticosti Island, Québec (see *Discussion,* p. 53). It may also occur in the Grande Coupe beds (Upper Ordovician, Ashgill, pre-Hirnantian) of the Matapédia Group on the Gaspé Peninsula, Québec, and in the Manitoulin Formation (Rhuddanian) of southern Ontario. *Propora speciosa* is found in the Ellis Bay Formation and possibly in the Grande Coupe beds (see *Discussion,* pp. 60, 61). It may also be present in the Tsagan-Del beds (Ashgill) of Mongolia, and in the Porkuni Stage (Hirnantian; *i.e.,* upper Gamachian) of Estonia. The Edgewood favositid *Paleofavosites subelongus* possibly occurs in basal strata of the Becscie Formation (see *Discussion,* p. 87). Thus, tabulate corals are consistent with the interpretation that strata containing the Edgewood Assemblage in the east-central United States are Gamachian to early Rhuddanian in age.

In northeastern Illinois, colonial corals of the Silurian assemblage appear in the lower Elwood Formation (see Text-fig. 6). This is above a bed in the underlying Wilhelmi Formation that contains Early Llandovery

Table 2.—Colonial corals of the Silurian assemblage in the study region, east-central United States.

- Subclass Tabulata
  - Order Heliolitida
    - Family Proporidae
      - *Propora thebesensis*
      - *Propora speciosa*
      - *Propora* sp. aff. *P. affinis*
      - *Propora* sp. A
  - Order Halysitida
    - Family Halysitidae
      - *Halysites* sp. cf. *H. alexandricus*
      - *Halysites*? sp. A
  - Order Favositida
    - Suborder Favositina
      - Superfamily Favositicae
        - Family Favositidae
          - Subfamily Favositinae
            - *Paleofavosites adaensis*
            - *Paleofavosites* sp. cf. *P. subelongus*
            - *Paleofavosites* sp. cf. *P. ivanovi*
            - *Paleofavosites* sp. A

graptolites possibly representing the earliest Rhuddanian *Parakidograptus acuminatus* Zone (Ross, 1962; Berry and Boucot, 1970, p. 145). The *Platymerella manniensis* brachiopod zone, which is considered to mark the Middle Llandovery (Berry and Boucot, 1970, pl. 2), begins in the upper Elwood (Willman, 1973, p. 14). In eastern Iowa, Early Llandovery graptolites in a bed near the base of the Mosalem Formation apparently represent the same zone as those in the Wilhelmi (Ross, 1964). The Mosalem as well as overlying strata have been placed in the Rhuddanian on the basis of correlations involving sea-level curves (Johnson *et al.*, 1985, fig. 5). Colonial corals characteristic of the Silurian assemblage appear in the upper Mosalem of northwestern Illinois, which has been correlated with the lower Elwood on the basis of solitary corals and stratigraphic position (McAuley and Elias, 1990, p. 26). We conclude that colonial corals of the Silurian assemblage appeared in the east-central United States during late Rhuddanian time, and underlying Silurian strata containing corals representing only the Edgewood Assemblage are early Rhuddanian in age.

A total of 11 of the 13 colonial coral species in the Edgewood Assemblage are known from Gamachian strata of the Leemon Formation in southern Illinois and southeastern Missouri, the Cason Shale in western north-central Arkansas, and the lower Keel Formation in south-central Oklahoma (*i.e.*, excluding Section-interval 24-3; see Text-fig. 2): *Propora thebesensis, Propora savagei, Propora speciosa, Acidolites* sp. A, *Protaraea* sp. A, *Halysites alexandricus, Catenipora lawrencica, Paleofavosites subelongus, Aulopora* sp. A, *Rhabdotetradium* sp. A, and *Palaeophyllum* sp. We consider them to have appeared in the east-central United States during latest Ordovician time. Three of the species, *P. thebesensis, H. alexandricus,* and *P. subelongus,* are known to range into the early Rhuddanian, when *Pycnostylus* sp. A appeared. These colonial corals occur in Section-intervals 32-1z and 32-1b of the Mosalem Formation (see Text-fig. 7), in association with the characteristic Edgewood solitary rugosan *Streptelasma subregulare* (see McAuley and Elias, 1990, p. 22; Elias, 1992, p. 120). Their stratigraphic position projects above a bed containing Early Llandovery graptolites near the base of the Mosalem at Section 26 (Bellevue) (see Elias, 1992, fig. 6).

In northeastern Missouri, the Edgewood species *Propora thebesensis, Propora savagei, Plasmopora* sp. cf. *P. logani,* and *Paleofavosites subelongus* occur in the Cyrene Formation near Edgewood, but their stratigraphic positions within the unit are unknown. The lower to middle portion of this formation is Gamachian, but the upper part may be Early Llandovery (see McAuley and Elias, 1990, pp. 17, 25, 26). Therefore, it is uncertain whether *Plasmopora* sp. cf. *P. logani* appeared during the latest Ordovician or the earliest Silurian. We consider specimens of *P. subelongus* from Section-interval 13-0 near the base of the Cyrene to be Gamachian (see Text-fig. 5). They occur below an interval containing the conodont *Noixodontus girardeauensis* (Satterfield) (see Thompson and Satterfield, 1975, fig. 11), which indicates a latest Ordovician age (see Barrick, 1986, pp. 64, 66). Strata of the Bryant Knob Formation that contain corals of the Edgewood Assemblage are tentatively considered to be Early Llandovery, although a Gamachian age cannot be ruled out (see McAuley and Elias, 1990, pp. 17, 26). Therefore, coralla of *P. subelongus* in the unnamed member and *P. thebesensis, P. savagei, Halysites alexandricus, Catenipora lawrencica, P. subelongus,* and *Palaeophyllum* sp. in the Kissenger Limestone Member are questionably early Rhuddanian.

In northeastern Illinois, we recovered a single colonial corallum from the sequence through the Wilhelmi Formation at Section 4 (Schweizer West) and Section 5 (Schweizer North). It was found in Section-interval 4-2, a small distance above a bed that contains Early Llandovery graptolites possibly representing the earliest Rhuddanian *Parakidograptus acuminatus* Zone (see Text-fig. 6). The coral is therefore assigned a Silurian age, but unfortunately can only be identified as *Paleofavosites* sp. indet. The characteristic Edgewood solitary rugosan *Streptelasma subregulare* is known to occur below the graptolite bed, and it is possible that those strata are Gamachian (see Elias, 1992, p. 118, fig. 4). The Edgewood colonial species *Propora the-*

besensis, Halysites alexandricus, Paleofavosites subelongus, and *Aulopora* sp. A are known from the Wilhelmi at other localities, but their stratigraphic positions with respect to the graptolite bed at Section 4 are unknown. These coralla are early Rhuddanian or questionably Gamachian in age.

The Bowling Green Dolomite of west-central Illinois and northeastern Missouri has been correlated with the lower Elwood Formation of northeastern Illinois, which is considered to be late Rhuddanian in age. Correlation of these strata is based on their position between units containing Edgewood Assemblage corals (below) and the *Platymerella manniensis* Zone (above), and on the occurrence in these strata of corals representing the Silurian assemblage (see McAuley and Elias, 1990, p. 26). *Paleofavosites* sp. cf. *P. ivanovi,* the only colonial coral known from the Bowling Green, is therefore considered to be late Rhuddanian. As is the case for corals, there appears to be a significant difference in brachiopod assemblages between the Bowling Green Dolomite and the underlying Bryant Knob Formation (see Stanton *et al.,* 1990).

The lower part of the Sexton Creek Limestone in southern Illinois and southeastern Missouri could be the same age as the Bowling Green Dolomite in west-central Illinois and northeastern Missouri (*i.e.,* Early Llandovery, late Rhuddanian). Both contain conodonts representing the *Paltodus dyscritus* fauna (Thompson and Satterfield, 1975, figs. 6, 7, 9, 11–15) and solitary rugose corals of the Silurian assemblage (McAuley and Elias, 1990, p. 26). *Stricklandia protriplesiana* (Amsden) has been identified from the Sexton Creek by Amsden (1974, p. 24; 1986, p. 26; 1988, p. 26). The presence of this brachiopod suggests a younger age (Late Llandovery, C_{1-2}), but its stratigraphic position within the formation is not known. The colonial corals *Propora* sp. A, *Halysites* sp. cf. *H. alexandricus, Halysites*? sp. A, and *Paleofavosites adaensis* occur in the Sexton Creek. They represent the Silurian assemblage, but their stratigraphic positions are unknown. *Paleofavosites adaensis* is also present in the upper Mosalem Formation of northwestern Illinois, suggesting correlation with those strata, which are considered to be late Rhuddanian. An upper limit on the range of *P. adaensis,* however, has not been established. The lower Sexton Creek is questionably assigned a late Rhuddanian age.

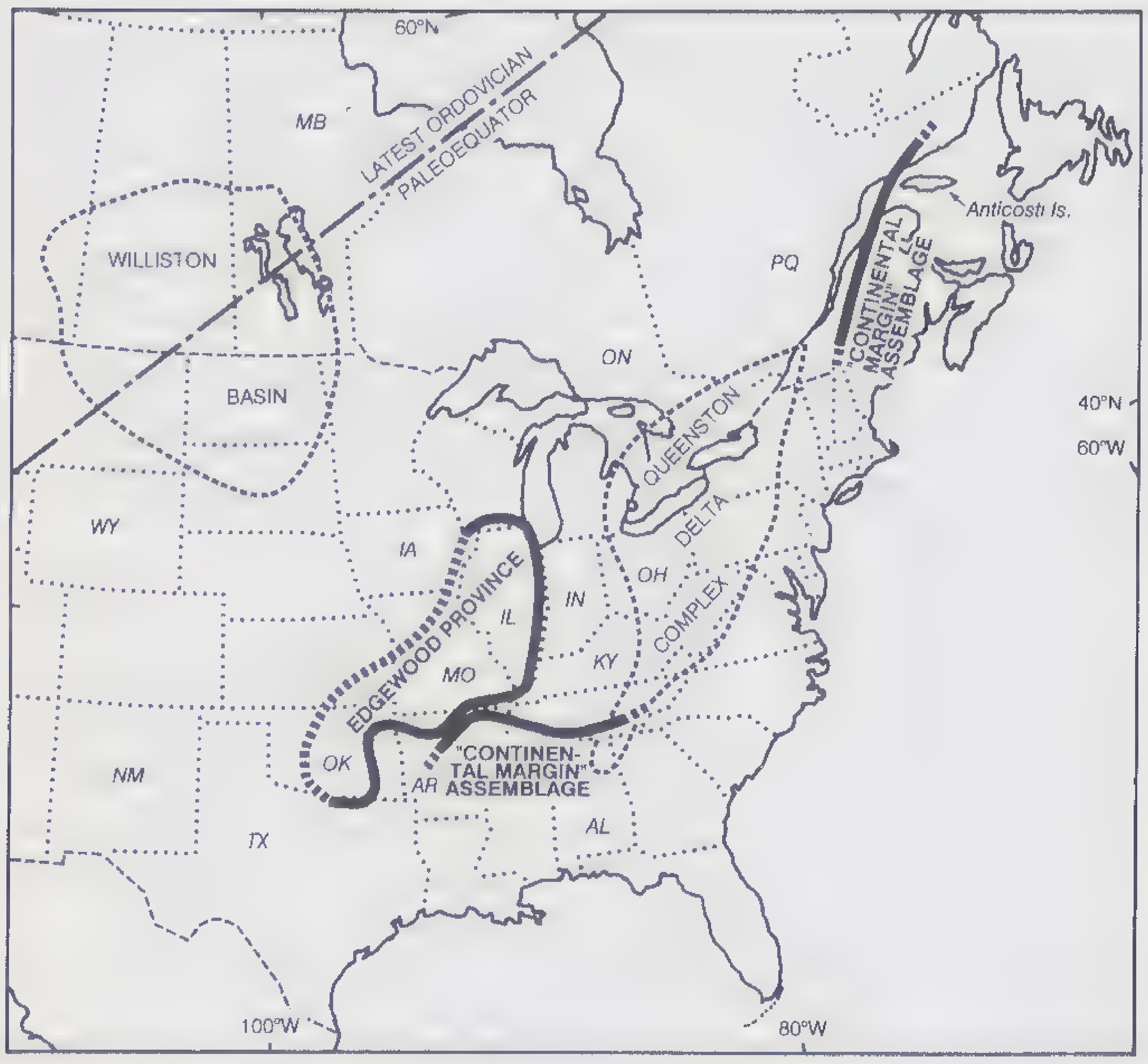
In the upper Keel Formation of south-central Oklahoma (Section-interval 24-3; see Text-fig. 2), the Edgewood colonial coral *Halysites alexandricus* occurs with the solitary rugosan *Streptelasma subregulare* (see Elias, 1992, p. 114, fig. 2). A conodont fauna of general Silurian aspect that appears in the same bed was considered to be Llandovery by Barrick (1986, p. 67), although a latest Ordovician age cannot be ruled out (see Bergström and Boucot, 1988, pp. 278, 279; McAuley and Elias, 1990, pp. 8, 9). Therefore, we consider the corallum of *H. alexandricus* from that interval to be of questionable early Rhuddanian age. In the east-central United States, the change in conodont faunas from those of Ordovician to those of Silurian aspect occurred during the range of the Edgewood coral assemblage, prior to the appearance of corals representing the Silurian assemblage.

Basal strata of the Cochrane Formation in south-central Oklahoma are evidently diachronous. Conodonts at the base of the formation, including those at Section 21 (Rock Crossing) and Section 23 (Lawrence Quarry), were considered to be Llandovery (position uncertain) by Barrick (1986, pp. 57, 64, 67). At Section 21, the characteristic Edgewood solitary rugosan *Streptelasma subregulare* occurs in the basal Cochrane (Elias, 1992, p. 114, fig. 2); unfortunately, we did not find colonial corals in the lower Cochrane at that locality. Assuming those strata are Llandovery (and not Gamachian), an early Rhuddanian age is indicated. *Paleofavosites adaensis,* the only colonial coral known from the lower Cochrane, represents the Silurian assemblage. It occurs at Section 23 and Section 35 (Henry House Falls), where solitary rugose corals in the basal Cochrane also represent the Silurian assemblage (see McAuley and Elias, 1990, p. 26, fig. 2; Elias, 1992, pp. 114, 115, fig. 2). The presence of *P. adaensis* suggests correlation with the upper Mosalem Formation of northwestern Illinois and the Sexton Creek Limestone of southern Illinois, and an age of late Rhuddanian (or possibly younger).

BIOGEOGRAPHY AND EVENTS

EDGEWOOD PROVINCE

The Edgewood Assemblage of colonial corals is strikingly different from typical Late Ordovician Richmondian assemblages in the North American cratonic interior, such as those known from the Richmondian Stage in Kentucky–Indiana–Ohio, the Cutter Dolomite in southern New Mexico–westernmost Texas, the Stony Mountain Formation in southern Manitoba, and the Churchill River Group in northeastern Manitoba (see Elias and Young, 1992, table 2; Text-fig. 9). Tabulates of the order Sarcinulida Sokolov (primarily *Calapoecia* Billings) and massive rugosans of the family Stauriidae Milne-Edwards and Haime (*Cyathophylloides* Dybowski and *Favistina* Flower) are widespread in the Richmondian but absent from the Edgewood Assemblage. *Propora* and *Halysites* are characteristic of the Edgewood Assemblage, but absent from the Richmondian assemblages. The Edgewood colonial rugo-



Text-figure 9.—Biogeographic and paleogeographic features in eastern and central North America. Latest Ordovician to earliest Silurian Edgewood Province and occurrences of Late Ordovician "continental margin" coral assemblages are shown; heavy solid and dashed lines represent established and uncertain boundaries, respectively. Late Ordovician Queenston Delta Complex and Williston Basin are outlined. Latest Ordovician paleoequator is based on Scotese and McKerrow (1990, fig. 9); present latitudes and longitudes are shown at margin. Abbreviations of states (United States): *AL* = Alabama, *AR* = Arkansas, *IA* = Iowa, *IL* = Illinois, *IN* = Indiana, *KY* = Kentucky, *MO* = Missouri, *NM* = New Mexico, *OH* = Ohio, *OK* = Oklahoma, *TX* = Texas, *WY* = Wyoming. Abbreviations of provinces (Canada): *MB* = Manitoba, *ON* = Ontario, *PQ* = Québec (Anticosti Island is identified).

sans, *Palaeophyllum* Billings and *Pycnostylus* Whiteaves, are fasciculate.

We relate the disappearance of Richmondian-type colonial corals from the cratonic interior of eastern North America to habitat loss. This resulted from westward progradation of the Queenston Delta Complex (Text-fig. 9) and from regression of the epeiric sea during a major glacio-eustatic drop in the late Richmondian. Extinctions among other groups in this region have also been linked to these events: brachiopods (Sheehan, 1973), solitary corals (Elias, 1982, pp. 48, 51; 1989; McAuley and Elias, 1990, p. 27), bryozoans (Anstey, 1986), and crinoids (Eckert, 1988). Erosional relief on the Richmondian surface of the Maquoketa Group is more than 30 m in northeastern Illinois (Willman, 1973, p. 12; Mikulic *et al.*, 1985, p. 9) and exceeds 40 m in eastern Iowa (Brown and Whitlow, 1960, p. 23; Whitlow and Brown, 1963, p. 11; see also Witzke and Kolata, 1988, pp. 61, 64, figs. 4, 5). The channels or depressions were subsequently infilled with latest Ordovician (?; Gamachian?) to earliest Silurian (Early Llandovery, Rhuddanian) deposits of the Wilhelmi and Mosalem formations. This suggests a period of emergence, at least within the northern portion of the study region in the east-central United States.

The Edgewood colonial corals *Propora savagei, Halysites alexandricus,* and *Catenipora lawrencica* are endemic, as are all solitary rugosans of the Edgewood Assemblage. The area of the east-central United States that was occupied by the Edgewood Assemblage has been named the Edgewood Province (Elias, 1982, pp. 47, 51, 52, fig. 24; McAuley and Elias, 1990, pp. 27, 28, fig. 11; Text-fig. 9). Corals were likely introduced to this biogeographic province from the continental margin, or were derived from forms previously restricted to the continental margin. *Propora,* which is present in the Richmondian Vauréal Formation on Anticosti Island, Québec (Bolton, 1981a, p. 107), appeared earlier along the continental margin than in the east-central United States. *Propora thebesensis* and *Propora speciosa* occur on Anticosti Island and in the Edgewood Province, indicating connection between the continental margin and cratonic interior. The endemic Edgewood species *Propora savagei* may have arisen from *P. thebesensis* by speciation within this province. *Halysites alexandricus* represents a genus that was introduced from elsewhere, as *Halysites* is known from earlier deposits only in Australasia (see *Discussion,* p. 70).

The Edgewood Assemblage includes the youngest North American representative of the order Tetradiida Okulitch (*Rhabdotetradium* sp. A), which is present in the latest Ordovician (Gamachian) Leemon Formation. This is among the youngest occurrences worldwide of this important Ordovician order. The Edgewood Assemblage also includes a number of first occurrences of typical Silurian taxa. The earliest North American member of the genus *Halysites* (*H. alexandricus*) appears in Gamachian strata within the Edgewood Province. The oldest definite representative of the family Plasmoporidae Sardeson (*Plasmopora* sp. cf. *P. logani*) is from Gamachian or questionably early Rhuddanian strata of the Cyrene Formation. The earliest known occurrence of the family Pycnostylidae Stumm (*Pycnostylus* sp. A) is from an early Rhuddanian bed within the Mosalem Formation.

Gamachian strata in the southern to central portion of the Edgewood Province were likely deposited during minor transgressions into the cratonic interior from the south, as sea level fluctuated during a regressive phase corresponding to the latest Ordovician glacial maximum (see Elias, 1982, pp. 51, 52; McAuley and Elias, 1990, p. 27). Immigration of colonial corals was probably related to shifts of suitable habitat areas during a time of depressed temperatures, as suggested previously for the solitary rugosans (Elias, 1989, p. 325). Corals that were introduced to the cratonic interior may have favored cooler water than did those in the Richmondian epeiric seas. Conditions were apparently within the warm, tropical to subtropical range, however, as indicated by widespread oölites and algal limestones, and the development of small biohermal mounds composed of bryozoans, brachiopods, and solitary rugose corals in the Leemon Formation at Section 19 (New Wells) in southeastern Missouri (Amsden, 1974, pp. 21, 22, fig. 17; 1986, pp. 33, 45, 54; Elias, 1989, p. 320). In the northern part of the Edgewood Province, sediment infilling channels or depressions cut into the Maquoketa Group probably accumulated during the major transgression associated with deglaciation, in latest Gamachian to Early Llandovery time (see Johnson *et al.,* 1985, fig. 5, eastern Iowa). Dispersion of Edgewood corals was evidently related to expansion of suitable habitat areas during the early phase of this event (Elias, 1989, pp. 320, 325).

The striking difference we have documented between the Edgewood Assemblage and typical Richmondian colonial coral assemblages in the North American cratonic interior probably reflects, at least in part, a hiatus between Richmondian and Gamachian deposition in the east-central United States. The most fossiliferous and complete Richmondian through Lower Llandovery sequence is in a continental margin setting on Anticosti Island, Québec (see Barnes, 1988). There, Elias and Young (1992, table 2) tabulated occurrences of corals in the Vauréal Formation (Richmondian), Ellis Bay Formation (Gamachian to possibly lowermost Rhuddanian), and lower portion of member 1 of the Becscie Formation (lower Rhuddanian). Some of the Richmondian species survived into the Gamachian. These include the massive stauriid *Cyathophylloides lyterion* Bolton and the sarcinulid *Calapoecia anticostiensis* Billings, which range from the Vauréal into the Ellis Bay and lowermost Becscie, respectively.

The Stonewall Formation overlies the Richmondian Stony Mountain Formation in southern Manitoba, within the Williston Basin area of the cratonic interior (Text-fig. 9). The Stonewall coral assemblage is a mixture of Richmondian types and newly introduced forms (see Elias, 1989, p. 322, fig. 3; Elias and Young, 1992, table 2). Sarcinulids (including *Calapoecia*) occur with one of the earliest North American representatives of the family Tryplasmatidae Etheridge (*Tryplasma* Lonsdale). Within the Williston Basin, the Stonewall Formation contains the youngest *Calapoecia* and the oldest *Propora.* All the colonial rugosans are fasciculate (*Palaeophyllum* and *Tryplasma*). The Stonewall assemblage has some similarities with the Edgewood Assemblage and with the Ellis Bay–lowermost Becscie assemblage.

On the basis of conodont biostratigraphy, Sweet (1979, p. 54, fig. 4; 1984, p. 33) concluded that uppermost strata of the Bighorn Group in Wyoming, which are probably equivalent to beds in the lower Stonewall Formation, are of post-Richmondian Ordovician age (*i.e.,* Gamachian). The position of the Ordovician–Silurian boundary in the Williston Basin is uncertain, but has been placed at the top of the Stonewall (Stearn, 1956, pp. 14–16) and at the *t* marker bed within the formation (Brindle, 1960, pp. 18, 19). On the basis of sequence stratigraphy and sea-level curves, the upper Stonewall and overlying lower Fisher Branch Formation were assigned to the Rhuddanian by Johnson and Lescinsky (1986, fig. 6). We consider the Stonewall coral assemblage to be consistent with an age assignment of Gamachian, or possibly latest Richmondian, to earliest Rhuddanian, and with an interpretation that the latest Ordovician to earliest Silurian sequence in the Williston Basin lacks significant hiatuses.

SILURIAN ASSEMBLAGE

Colonial corals are uncommon in strata immediately above those containing the Edgewood Assemblage in the east-central United States. The Silurian assemblage found in these overlying rocks is composed of the same three genera that are dominant in the Edgewood: *Paleofavosites, Propora,* and *Halysites.* We infer that at least some of the characteristic species were likely derived from Edgewood forms. For example, *Paleofavosites* sp. cf. *P. subelongus* probably arose from *P. subelongus* through the appearance of rare mid-wall pores. *Halysites* sp. cf. *H. alexandricus,* in which tabulae are commonly strongly concave, could have descended from *H. alexandricus,* which has flat to slightly concave or convex tabulae. Some species in the Silurian assemblage may have been introduced from elsewhere, or perhaps were derived from forms in other areas. For example, *Paleofavosites* sp. cf. *P. ivanovi* is comparable to *P. ivanovi* in the Upper Ordovician of the Urals and Siberian Platform (see *Discussion,* p. 95).

The change from colonial corals of the Edgewood Assemblage to those of the Silurian assemblage is generally abrupt (see Text-fig. 8, foldout inside back cover). It usually occurs between formations, at a distinct unconformity or contact that could represent a hiatus. In northwestern Illinois, however, the changeover occurs within the Mosalem Formation, and the record of the critical time interval may be most complete. The only known overlap of Edgewood and Silurian species occurs in this area, at Section 32 (Thomson East) (see

Text-fig. 7). There, Edgewood colonial and solitary corals occur in the fill of small, local channels (Section-interval 32-1b) and in strata lateral to the channels (including the coral-rich bed, Section-interval 32-1z) (see also McAuley and Elias, 1990, p. 22; Elias, 1992, p. 120). Above the filled channels (Section-interval 32-1c), *Paleofavosites* sp. cf. *P. subelongus* and all solitary rugosans represent the Silurian assemblage. Two other species in that interval also occur in the Edgewood Assemblage. *Propora thebesensis* is known to range as high as 1.35 m above the base of the interval, and *Propora speciosa* was found 0.7 m above the base. The coral-rich bed and channels suggest a period of nondeposition and local erosion, possibly recording a minor regressive event (see McAuley and Elias, 1990, p. 23; Elias, 1992, p. 120). This occurred during the worldwide transgression in the earliest Silurian (Early Llandovery, Rhuddanian), which was related to deglaciation (see Johnson *et el.,* 1985, fig. 5, eastern Iowa).

The changeover from Edgewood to Silurian assemblages took place as water depth and temperature were generally increasing during the Early Llandovery (McAuley and Elias, 1990, p. 29; Elias, 1989, p. 325). Nevertheless, corals representing the Silurian assemblage appear above local channels within the Mosalem Formation and above unconformities or formational boundaries elsewhere, suggesting that the faunal change followed a regressive event. We infer that as areas in the east-central United States became inhospitable, geographic ranges of Edgewood corals were reduced. Most species became extinct; some colonial corals apparently underwent rapid evolution, probably in small populations. The descendants dispersed and new immigrants arrived as suitable habitat areas expanded when the Early Llandovery transgression resumed. A few Edgewood colonial species evidently survived briefly in local refugia. It is noteworthy that, unlike the colonial corals, all solitary rugosans known from the Silurian assemblage are immigrants that represent genera different from those in the Edgewood Assemblage (McAuley and Elias, 1990, table 1; Elias, 1992, p. 120). Corals of the Silurian assemblage probably favored somewhat deeper, possibly warmer water than those of the Edgewood Assemblage.

THE EDGEWOOD COLONIAL CORALS: TAPHONOMY AND PALEOECOLOGY

INTRODUCTION

In this section, we examine the taphonomy and paleoecology of colonial corals in the Edgewood Assemblage, and their relationship to paleoenvironmental factors. Corallum abrasion and orientation are shown to reflect the energy level. The development of composite coralla is related to substrate stability. Encrusting corals, as well as encrusters on and borings within coralla, provide records of interactions among species. Encrusting relationships are used as indicators of substrate availability and stability, sedimentation rate, and turbidity. Corallum growth forms and growth rates are related to sedimentation rate and substrate stability; corallum size may reflect environmental stability. We conclude this section with an overview of paleoenvironments inhabited by colonial corals in the Edgewood Province, and a synthesis providing detailed paleoenvironmental determinations for stratigraphic units and localities, based on comparative taphonomy and paleoecology.

ABRASION

Abrasion of colonial coralla has rarely been considered in a paleoenvironmental context (Young, 1988, pp. 24, 25). As demonstrated for solitary rugosans (Elias *et al.,* 1988, pp. 23, 24), the degree of abrasion reflects the intensity and duration of abrasive processes. It therefore provides an indication of the energy level and sedimentation rate before final burial.

In this study, Edgewood colonial coralla are categorized as nonabraded or abraded based on examinations of their exterior surfaces in thin sections. Specimens selected for this analysis are nonweathered, well preserved, enclosed in matrix, and lack obvious stylolitized boundaries. We consider coralla to have been abraded prior to final burial if their bases are absent (Pl. 3, figs. 4, 8) and/or if calices are clearly reduced or removed completely from some or all of the upper surfaces (Pl. 14, fig. 10, Pl. 16, fig. 12); this is particularly obvious if tabulae or dissepiments are truncated. Samples of sufficient size for comparative purposes are obtained by combining data from all suitable massive tabulates in each of five collections (Table 3); these represent the orders Favositida Wedekind and Heliolitida Frech. The proportion of abraded coralla in any collection does not appear to differ between the two numerically important species, *Paleofavosites subelongus* and *Propora thebesensis.*

In the Edgewood Province, we observe minimal damage due to abrasion only in specimens from the coral-rich bedding surface in the Mosalem Formation at Section 32 (Thomson East). The proportion of abraded coralla is low in this bed (Table 3). The mudstone to wackestone lithology suggests low energy conditions.

All or the vast majority of specimens are abraded in the *Brevilamnulella* beds of the Keel Formation at Section 23 (Lawrence Quarry), the Leemon Formation

Table 3.—Conditions, orientations, and types of tabulate coralla in selected units within the Edgewood Province. Coralla with axes of growth within 20° of vertical are considered to be in growth orientation; those with axes more than 20° from vertical are considered to be overturned. Composite coralla show one or more marked changes in direction of growth; noncomposite coralla do not.

units	*conditions (massive coralla)*		*orientations (massive coralla)*		*types of coralla*	
section-intervals	*nonabraded*	*abraded*	*growth*	*overturned*	*noncomposite*	*composite*
Keel Fm., *Brevilamnulella* beds						
23-2	1 (7%)	13 (93%)	3 (19%)	13 (81%)	29 (100%)	0 (0%)
Keel Fm., oölite						
23-2a, 23-3, and 23a-1	—	—	—	—	14 (88%)	2 (12%)
Leemon Fm.						
31-1 and 31-1b	1 (5%)	18 (95%)	—	—	23 (82%)	5 (18%)
Bryant Knob Fm., Kissenger Lst. Mbr.						
14-1	3 (9%)	32 (91%)	5 (21%)	19 (79%)	73 (99%)	1 (1%)
15-1	0 (0%)	14 (100%)	—	—	33 (100%)	0 (0%)
Mosalem Fm., coral-rich bedding surface						
32-1z	9 (82%)	2 (18%)	8 (44%)	10 (56%)	53 (100%)	0 (0%)

at Section 31 (Thebes North), and the Kissenger Limestone Member of the Bryant Knob Formation at Section 14 (Higginbotham Farm) and Section 15 (Calumet) (Table 3). The amount of damage to individual coralla appears to be greatest at Section 31, followed by Sections 14 and 15. The packstone to grainstone lithologies of all these units suggest higher energy conditions than at Section 32 (Thomson East). The proportions of nonabraded and abraded coralla at Section 32 and Section 14 are significantly different ($\chi^2 = 19.644$; $\chi^2_{0.05} = 3.841$, 1 d.f.). It appears that massive tabulate coralla in the Edgewood Province became abraded in all but the lowest energy environments.

Orientation

Attitudinal disorientation of objects such as colonial corals and stromatoporoids is most likely to have resulted from toppling or transportation by wave and current energy (Jackson, 1983, p. 86; Kershaw, 1984, pp. 125–127; Harrington, 1987, pp. 660, 661). A number of other mechanisms have also been proposed, including buckling as a result of pressures within reefs (Manten, 1971, p. 435), bioturbation and predation (Kershaw, 1984, p. 125), weakening of cemented bases by boring, and substrate instability caused by growth (Kobluk *et al.*, 1977, p. 2229). There are diagnostic features that allow recognition of possible occurrences of most of these mechanisms; the absence of such features allows us to examine the relationship between orientation and environmental energy. We use data from massive Edgewood tabulates in our analyses; these represent the families Favositidae Dana and Proporidae Sokolov. None of the specimens is attached to an object large enough to have affected orientation, and all these corals inhabited unlithified substrates.

Where possible, attitudinal orientations of Edgewood colonial coralla with respect to bedding were marked in the field and confirmed later using thin sections. Because the data set is small, we recognize just two classes; those in growth orientation and those that are overturned (disoriented). Coralla in which the growth direction differs by more than 20° from upright are considered to be overturned. We follow Philcox (1971, p. 344) in distinguishing the terms "growth orientation" and "growth location."

Most coralla are overturned in each of the three collections from which sufficient data are available for comparison (Table 3). Although attitudinal orientations do not differ significantly between the intervals (χ^2 tests), it is noteworthy that a smaller proportion is overturned on the coral-rich bedding surface of the Mosalem Formation at Section 32 (Thomson East) than in the *Brevilamnulella* beds of the Keel Formation at Section 23 (Lawrence Quarry) or the Kissenger Limestone Member of the Bryant Knob Formation at Section 14 (Higginbotham Farm). That might be expected considering the lower energy conditions indicated by the mudstone to wackestone lithology and high proportion of nonabraded coralla at Section 32, compared with the packstone to grainstone lithologies and high proportions of abraded coralla at the other sections.

It must be remembered, however, that differences in attitudinal orientations between collections do not *necessarily* indicate different environmental energies. Simple comparisons ignore important variables such as skeletal density, size, growth form, and substrate morphology and consistency (see Kershaw, 1984, pp. 125–127). The problem of density can be overcome by limiting analyses to coralla of comparable structure.

Table 4.—Orientations of massive Edgewood tabulate coralla in various size and growth form categories. Coralla with axes of growth within 20° of vertical are considered to be in growth orientation; those with axes more than 20° from vertical are considered to be overturned.

	orientations	
categories	*growth*	*overturned*
corallum sizes		
10.5–30.0 mm	3 (19%)	13 (81%)
30.5–50.0 mm	7 (30%)	16 (70%)
50.5–70.0 mm	5 (50%)	5 (50%)
growth forms		
columnar	0 (0%)	5 (100%)
high bulbous	3 (27%)	8 (73%)
low bulbous	1 (20%)	4 (80%)
high domical	6 (35%)	11 (65%)
low domical	5 (45%)	6 (55%)

The spacing and thickness of skeletal elements in the Edgewood favositids and proporids appear to be approximately equivalent.

Little attention has been given to the relationship between corallum size and attitudinal orientation. It might be expected that, other things being equal, small coralla would be overturned more easily than large ones. In an analysis of hemispherical tabulates and stromatoporoids, Kobluk *et al.* (1977) concluded that there was no difference in the sizes of oriented and disoriented specimens, possibly because energy levels involved in the disorientation process were so high that all specimens were affected. Harrington (1987, p. 660), however, argued that the data of those authors suggest "a slight tendency toward more frequent disorientation of smaller individuals."

In the present study, attitudinal orientations are compared for three size categories of massive Edgewood tabulates (favositids and proporids), using average linear dimension (*i.e.*, (maximum width + height) ÷ 2; see *Corallum Size*, p. 32) as a measure of size (Table 4). The proportion of coralla in growth orientation increases with increased size, although there are too few specimens to confirm this statistically. Such a pattern suggests that at least some coralla in growth orientation are in fact in growth location. If all specimens had been transported, the proportion deposited in growth orientation would not be expected to differ among size classes, other things being equal.

Growth form will affect the probability of disorientation because objects such as colonial corals and stromatoporoids with lower forms are apparently less likely than tall ones to be overturned by currents or waves (Manten, 1971, p. 437; Harrington, 1987, p. 660; Kershaw, 1990, p. 699). Nevertheless, it appears from flume experiments that stromatoporoids with laminar shapes are more readily overturned than those with low domical forms (Kershaw, 1984, p. 125). Domical forms are most likely to be deposited in growth orientation following transportation because that is the most stable attitude (Abbott, 1974, p. 8), but they may also be overturned 180°. Columnar forms are most stable when disoriented 90°, with their long axes parallel to bedding (Hodges and Roth, 1986, p. 1153).

We compare attitudinal orientations of massive Edgewood tabulates (favositids and proporids) using five growth form categories (see *Growth Form*, pp. 27, 28) (Table 4). All columnar coralla are overturned. Proportions of coralla in growth orientation are intermediate for high and low bulbous forms and high domical forms. As expected, the proportion in growth orientation is highest for low domical coralla, although there are too few specimens to confirm these patterns statistically.

The possible effects of corallum size and growth form on attitudinal orientation should be taken into account when comparing data from different localities or units for the purpose of inferring environmental energy levels. We therefore recommend that comparisons be done within the classes of a standardized set of size groupings for each growth form category. Unfortunately, there are insufficient data to conduct such an analysis in the Edgewood Province.

Substrate morphology is an important variable in orientation analysis because of its relationship to the stability and mobility of objects such as corals and stromatoporoids (Kershaw, 1984, p. 125). Movement can be inhibited if coralla are closely spaced. That may account in part for the comparatively high proportion of specimens in growth orientation on the coral-rich bedding surface at Section 32 (Thomson East). Overturned domical forms are more likely to be preserved in an inverted position, rather than be reoriented into the more stable growth orientation, if lodged against other objects (Abbott, 1974, p. 12). Overturned coralla in contact with other specimens were observed on the coral-rich bedding surface at Section 32. The effects of substrate stability on coral orientation are considered under *Composite Coralla*, below.

COMPOSITE CORALLA

In this study, use of the term "composite" follows Young and Scrutton (1991, p. 371); it is restricted to coralla that show one or more marked changes in the direction of growth, as observed in longitudinal section (*e.g.*, Pl. 5, fig. 8). Philcox (1971, p. 341) used the term in a broader sense, including coralla in which regeneration was not accompanied by changes in growth direction. Redirected growth records a change in orientation during the life of the colony (Jackson, 1983, p. 86); the event causing disorientation was not severe enough to effect mortality by abrasion, burial, or transportation. Scouring of the sediment supporting unattached coralla could result in decreased stability and in overturning, leading to the development of composite forms. The ease with which sediment can be eroded is related to its cohesion. Sand is typically less cohesive than mud and can be eroded at relatively low current velocities (Potter *et al.*, 1980, p. 11); it therefore generally forms a less stable substrate.

Data from representatives of the orders Favositida, Heliolitida, and Halysitida Sokolov in the Edgewood Province (Table 3) support the interpretation that formation of composite coralla is related to substrate stability. Composite specimens are most common in the Leemon Formation at Section 31 (Thebes North) and in oölites of the Keel Formation at Section 23 (Lawrence Quarry). Lithologies at both localities suggest sandy sediments of low cohesion. Coralla from Section 31 are in a skeletal grainstone with moderately well-rounded grains (see Amsden, 1986, pl. 1, fig. 2), and those from Section 23 are in an oölitic grainstone (see Amsden, 1960, pl. 10, figs. 5, 6; 1986, pl. 6, fig. 1).

The proportion of composite coralla in the Kissenger Limestone Member of the Bryant Knob Formation at Section 14 (Higginbotham Farm) is significantly lower than that in the Leemon Formation at Section 31 (Thebes North) ($\chi^2 = 7.237$; $\chi^2_{0.05} = 3.841$, 1 d.f.). The pronounced alignment of clasts in the fossiliferous grainstone at Section 14 may have resulted in greater substrate stability. Composite specimens are absent in grainstone of the Kissenger Limestone at Section 15 (Calumet); this is significantly different from the proportion at Section 31 ($\chi^2 = 4.265$; $\chi^2_{0.05} = 3.841$, 1 d.f.). Composite coralla are also absent in the *Brevilamnulella* beds of the Keel Formation at Section 23 (Lawrence Quarry). The alignment of brachiopod shells in that oölitic, bioclastic packstone to grainstone may have increased substrate stability (see Amsden, 1986, pl. 2, fig. 1, pl. 3, fig. 2). The absence of composite colonies on the coral-rich bedding surface of the Mosalem Formation at Section 32 (Thomson East) is significantly different from Section 31 ($\chi^2 = 7.239$; $\chi^2_{0.05} = 3.841$, 1 d.f.). The mudstone to wackestone lithology at Section 32 suggests that sediment cohesion was relatively high.

Encrusting Relationships

Analysis of encrusting relationships involving colonial corals provides information about the duration of exposure of skeletal material. This is useful in determining environmental factors such as sedimentation rate and substrate availability and stability. Such analysis also sheds light on the paleobiology of corals and other encrusters, and on interactions among species.

In this study, the term "encruster" is applied to all organisms that grew initially on hard substrates, even if most subsequent growth was vertical. It is not restricted to those having primarily laminar or runner forms (*cf.*, Taylor, 1990, pp. 346, 347). Examinations of thin sections reveals that Edgewood colonial corals were involved in a variety of encrusting relationships. They were both substrates for encrusting organisms including other corals, and active encrusters of coralla and other objects.

Coatings of micritic, thrombolitic, and rarely *Girvanella*-like forms, presumed to be of algal origin, are the most common type of encrustation on Edgewood colonial coralla. We have observed them on *Propora thebesensis, Protaraea* sp. A, *Halysites alexandricus, Paleofavosites subelongus,* and *Palaeophyllum* sp. Such coatings generally cover a large portion of the corallum surface, which was usually abraded prior to encrustation. The algae do not seem to have been host-specific, and evidently became associated with coralla during or following post-mortem transport (see also McAuley and Elias, 1990, p. 30). Algal-coated specimens are widely distributed in the Edgewood Province, but the proportion of colonial coralla with such encrustations is greatest in the *Brevilamnulella* beds of the Keel Formation at Section 23 (Lawrence Quarry) (Table 5).

Edgewood colonial coralla having attached animals are relatively common only in the *Brevilamnulella* beds and oölites of the Keel Formation at Section 23 (Lawrence Quarry) (Table 5). The most common encrusting animals are bryozoans, which are usually laminar in form and small. One bryozoan colony occurs on a specimen of *Palaeophyllum* sp. from the Kissenger Limestone Member of the Bryant Knob Formation at Section 14 (Higginbotham Farm) (Pl. 21, figs. 10–12), but all other bryozoans occur on *Halysites alexandricus.* We observed them on four coralla from the *Brevilamnulella* beds at Section 23, one from the Keel oölite at Section 23, one from the upper oölitic bed of the Keel at Section 24 (Coal Creek), and two from the Kissenger Limestone at Section 15 (Calumet).

Encrusting stromatoporoids have been observed on single coralla of *Propora thebesensis* (above an algal coating), *Protaraea* sp. A, and *Paleofavosites subelongus* from the *Brevilamnulella* beds of the Keel Formation at Section 23 (Lawrence Quarry), and on single specimens of *P. subelongus* from the Keel oölite at Section 23 and the unnamed member of the Bryant Knob Formation at Section 18 (Kissenger). A small, unidentifiable solitary rugosan occurs on a specimen of *Halysites alexandricus* from the *Brevilamnulella* beds

Table 5.—Encrusting relationships involving colonial corals in selected units within the Edgewood Province.

units *section-intervals (n = no. of coralla)*	*colonial coralla with encrusters*			*encrusting colonial corals*
	algal	*animal*	*all types*	
Keel Fm., *Brevilamnulella* beds				
23-2 (n = 29)	11 (38%)	8 (28%)	17 (59%)	7 (24%)
Keel Fm., oölite				
23-2a, 23-3, and 23a-1 (n = 11)	2 (18%)	3 (27%)	5 (45%)	1 (9%)
Leemon Fm.				
31-1 and 31-1b (n = 19)	0 (0%)	1 (5%)	1 (5%)	0 (0%)
Bryant Knob Fm., Kissenger Lst. Mbr.				
14-1 and 14-2 (n = 31)	4 (13%)	1 (3%)	4 (13%)	0 (0%)
15-1 (n = 23)	2 (9%)	2 (9%)	4 (17%)	0 (0%)
Mosalem Fm., coral-rich bedding surface				
32-1z (n = 45)	2 (4%)	0 (0%)	2 (4%)	0 (0%)

at Section 23. One corallum of the solitary rugosan *Keelophyllum oklahomense* McAuley and Elias from the Keel oölite at Section 23 is attached to *H. alexandricus* (in part above a thin encruster that is probably a bryozoan) (McAuley and Elias, 1990, pl. 12, fig. 4; Pl. 9, fig. 9). A probable tentaculitid occurs on a specimen of *H. alexandricus* from the Leemon Formation at Section 31 (Thebes North) (Pl. 10, fig. 4).

Encrusting colonial corals are relatively common in the *Brevilamnulella* beds of the Keel Formation at Section 23 (Lawrence Quarry) (Table 5). *Protaraea* sp. A, which is restricted to those beds, typically has a small, thin, tabular form. One specimen was observed to encrust both *Halysites alexandricus* (Pl. 8, fig. 12) and *Aulopora* sp. A, and another occurs on a stromatoporoid. One corallum of the large cateniform species *H. alexandricus* is attached to both *Protaraea* sp. A and a stromatoporoid (Pl. 9, fig. 8), and another encrusts the solitary rugosan *Streptelasma leemonense* Elias. Two specimens of the small cateniform species *Catenipora lawrencica* occur on *H. alexandricus,* and one of them is also attached to *S. leemonense. Aulopora* sp. A is a small coral with an irregular, low, reptant form. One example encrusts *H. alexandricus,* a stromatoporoid, and calcareous algae (Pl. 20, fig. 1).

Encrusting colonial corals are rare or absent elsewhere in the Edgewood Province (*e.g.,* Table 5). Single examples of *Paleofavosites subelongus* on stromatoporoids are known from the Keel oölite at Section 23 (Lawrence Quarry) and the unnamed member of the Bryant Knob Formation at Section 18 (Kissenger). One specimen of *P. subelongus* occurs on an algal crust in the Kissenger Limestone Member of the Bryant Knob (Section-interval 18-2). *Protaraea* sp. A, *Catenipora lawrencica,* and *Aulopora* sp. A are the only Edgewood colonial corals that seem to have been primarily encrusters. *Halysites alexandricus* and *P. subelongus* rarely had encrusting modes of life.

Most of the encrusting animals that colonized colonial coralla appear to have favored the lateral and upper surfaces of ranks in *Halysites alexandricus* as a substrate. This was probably because lacunae within the cateniform skeleton provided protected sites for colonization and the available surface area was high. One corallum of *H. alexandricus* from the *Brevilamnulella* beds at Section 23 (Lawrence Quarry) is encrusted in different places by a bryozoan, *Catenipora lawrencica, Aulopora* sp. A, and a solitary rugosan. Another is encrusted in different places by a bryozoan, *Protaraea* sp. A, and *C. lawrencica.* In most cases, animals attached to colonial coralla as well as encrusting colonial corals evidently grew on skeletons of dead hosts. Where multiple encrustation of the same substrate occurred, as in the *Brevilamnulella* beds of the Keel Formation at Section 23, there is generally evidence of reorientation and abrasion between colonization events.

In the Edgewood Province, colonial coralla with encrustations of all types are common only in the *Brevilamnulella* beds and oölitic beds of the Keel Formation at Section 23 (Lawrence Quarry) (Table 5). The proportion of encrusted coralla is significantly greater in the *Brevilamnulella* beds than in the Leemon Formation at Section 31 (Thebes North), the Kissenger Limestone Member of the Bryant Knob Formation at Section 14 (Higginbotham Farm) and at Section 15 (Calumet), and the coral-rich bedding surface of the Mosalem Formation at Section 32 (Thomson East) ($\chi^2 = 11.760, 11.829, 7.425,$ and 24.359, respectively; $\chi^2_{0.05} = 3.841$, 1 d.f.). Encrusting colonial corals are common only in the *Brevilamnulella* beds (Table 5). These patterns seem to reflect predictable limiting factors in the distribution of encrusters: substrate availability and stability, sedimentation rate, and turbidity.

Skeletal objects including relatively large colonial coralla that could have served as attachment sites for encrusters are abundant in the *Brevilamnulella* beds, which in places are coquinoid (see Amsden, 1986, p. 10). The aligned brachiopod shells and absence of composite colonial corals suggest a stable substrate favorable for attachment and subsequent growth. A low sedimentation rate would have provided sufficient time for numerous objects to become encrusted, and for multiple encrustation of some coralla. We describe the *Brevilamnulella* beds as "incipient biohermal." It seems that periodic overturning of coralla, perhaps during occasional storms, inhibited the development of complex, long-term encrusting relationships that could have led to the formation of bioherms. The lithology and relatively high frequency of composite coralla in the less fossiliferous Keel oölite suggest lower substrate availability and stability; the observed frequency of encrusted coralla is higher than might be expected. At least some of those coralla may have been transported from the *Brevilamnulella* beds.

The rarity of encrusting relationships in the Leemon Formation at Section 31 (Thebes North), where the frequency of composite corals is greatest, can be attributed to substrate instability and possibly also to a relatively high sedimentation rate. Encrusted colonial coralla are uncommon in the Kissenger Limestone Member of the Bryant Knob Formation. The alignment of clasts and rarity of composite coralla at Section 14 (Higginbotham Farm), and the absence of composite coralla at Section 15 (Calumet), suggest that substrate stability was comparatively high. Perhaps encrusters were hindered by relatively high sedimentation rates at those localities. Encrusting relationships are rare in the Mosalem Formation at Section 32 (Thomson East), where the mudstone to wackestone lithology suggests that encrusters may have been inhibited by turbid conditions.

BORINGS

Borings in coral skeletons, produced by soft-bodied organisms that are not otherwise preserved, add to the record of biodiversity. Analysis can reveal whether boring occurred during life or after death of the host. This provides information about the paleobiology of both the coral and the endolith.

In our examinations of Edgewood colonial coralla, we observed borings only in a single specimen of *Protaraea* sp. A from the *Brevilamnulella* beds of the Keel Formation at Section 23 (Lawrence Quarry). Microborings are abundant in thin sections of that corallum (Pl. 8, figs. 8–11). They are tubular, slightly curved or less commonly straight, and in some cases have randomly located low-angle bends. Branches may arise at irregular intervals and may be oriented at various angles. Bulbous enlargements of variable shape occur along some borings. Diameters of the tubular borings are generally 25 to 75 μm, but the largest tubular borings and bulbous enlargements are 400 μm across. Diameter may vary along the length of a boring. The maximum observed length is 3.75 mm. Terminations of tubular borings are rounded.

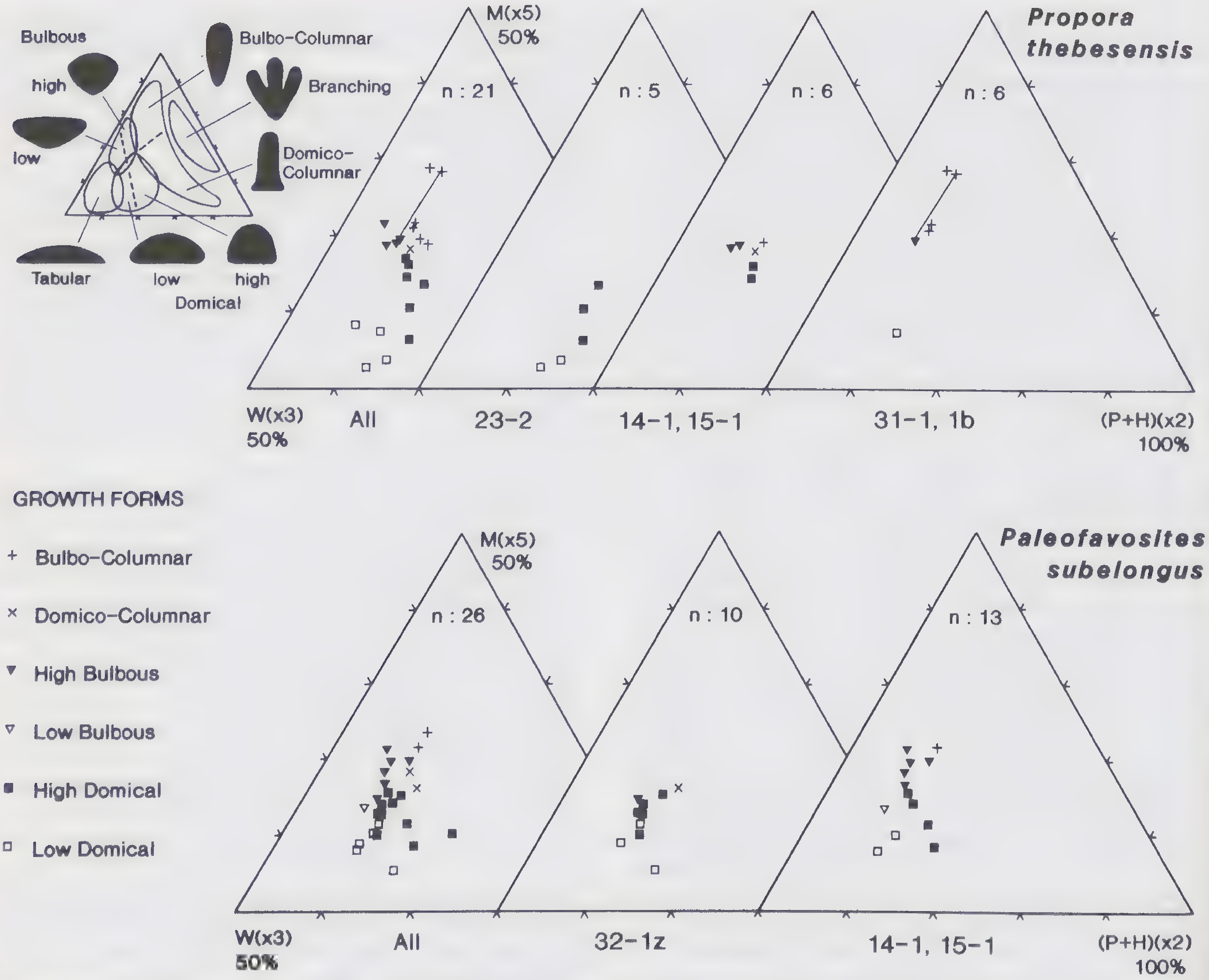
The smaller borings are filled with micritic material. Larger ones may be filled with micrite or more commonly have only a micritic lining, but micrite is absent in a few of the largest. Some of the borings penetrate into the calical and basal surfaces of the corallum. Most are located in the interior of the skeleton, where some penetrate upward or downward from regeneration surfaces, or follow along or cross such surfaces. There is a tendency for tubular borings to parallel trabeculae of the coral skeleton.

The morphology and size of these microborings are comparable to some of those in a Middle Ordovician stromatoporoid from Norway, documented by Pickerill and Harland (1984, figs. 3b, 3d). Such structures are considered to be of probable sponge origin (Pickerill and Harland, 1984, p. 889). *Protaraea* sp. A has the densest skeleton of any Edgewood coral. It is virtually solid, forming an ideal substrate for borers. The distribution and orientation of borings suggest that the corallum surface was colonized by endoliths between regeneration events, as well as following death of the coral and transportation of the skeleton.

GROWTH FORM

Based on our study of Edgewood tabulates, we are able to expand and refine the quantitative methods for analysis of colonial coral growth forms that were established by Young and Scrutton (1991). This permits detailed examination of ranges of variation, and comparison of subtle differences in form within and among stratigraphic units and localities. Various aspects of corallum growth form are related to sedimentation rate and substrate stability.

To document the growth forms of Edgewood tabulate coralla, lateral profiles of nonabraded or slightly abraded specimens are produced. Most coralla are enclosed in matrix; outlines of these are taken from polished longitudinal surfaces or from thin sections through the corallum growth axis. The following parameters are measured: corallum width (W), height (H), height to the widest point (M), and, if possible, perimeter (P) (see Young and Scrutton, 1991, p. 372, fig. 2a). Growth forms of coralla are defined using the system of Young and Scrutton (1991, pp. 370, 371). The categories include tabular ($W{:}H \geq 3{:}1$, base and upper surface subparallel; some coralla of *Protaraea* sp. A have this form), domical ($W{:}H \geq 1{:}1$ but $< 3{:}1$, $M < 0.5H$), bulbous ($W{:}H \geq 1{:}1$ but $< 3{:}1$, $M \geq 0.5H$), columnar



Text-figure 10.—Triangle diagrams showing growth forms of *Propora thebesensis* (top row) and *Paleofavosites subelongus* (bottom row). W = corallum width, H = corallum height, M = height to the widest point, P = corallum perimeter; the three values plotted are W (× 3) (range 0–50%), M (× 5) (range 0–50%), and (P + H) (× 2) (range 50–100%). Percentages are of the total for the three plotted values. For example, a corallum having W = 100 mm, H = 50 mm, M = 40 mm, and P = 250 mm would have values of W (× 3) = 300 (27.3%), M (× 5) = 200 (18.2%), and (P + H) (× 2) = 600 (54.5%); such a specimen would plot in the lower left part of the field for low bulbous growth forms shown in the small standard triangle diagram in the upper left of the text-figure. For each species, the plot for all measurable coralla from the east-central United States is identified; other plots are for the Section-intervals indicated; n = number of coralla (two parts of one composite corallum were considered separately). Each data point represents a single corallum, except where a solid line connects points from a composite corallum; symbols for growth forms are listed in the lower left of the text-figure. The small standard triangle diagram shows fields in which various growth form categories plot; lateral profiles of representative coralla are shown as silhouettes.

(W:H < 1:1, sides subparallel), and branching (*i.e.*, dendroid or digitate; no Edgewood coralla have this form). In addition, we subdivide columnar forms into two categories, domico-columnar (M < 0.5H) and bulbo-columnar (M ≥ 0.5H). We also define low and high categories for both domical and bulbous coralla by bisecting the field for those forms on graphs of corallum width *versus* height (*i.e.*, low, W:H ≥ 1.6:1 but < 3:1; high, W:H ≥ 1:1 but < 1.6:1).

Growth forms of specimens of *Propora thebesensis* and *Paleofavosites subelongus* for which the necessary parameters can be measured are plotted on triangle diagrams using the techniques of Young and Scrutton (1991, p. 373, fig. 3) (Text-fig. 10). Such diagrams permit graphical depiction of ranges of variation and subtle differences in form. Both species show similar degrees of variation, and both include domical, bulbous, and columnar coralla, but patterns of variation are not identical. Triangle diagrams for Section-interval 14-1 (Higginbotham Farm) and Section-interval 15-1 (Cal-

Table 6.—Corallum growth forms of selected tabulate species in units within the Edgewood Province.

units *section-intervals* *species (n = no. of coralla)*	*bulbous forms*			*domical forms*		
	bulbo-columnar	*high bulbous*	*low bulbous*	*domico-columnar*	*high domical*	*low domical*
Keel Fm., *Brevilamnulella* beds						
23-2						
Propora thebesensis (n = 6)	0 (0%)	0 (0%)	1 (17%)	0 (0%)	3 (50%)	2 (33%)
		1 (17%)			5 (83%)	
Leemon Fm.						
31-1 and 31-1b						
Propora thebesensis (n = 10[1])	7 (70%)	1 (10%)	0 (0%)	0 (0%)	0 (0%)	2 (20%)
		8 (80%)			2 (20%)	
Bryant Knob Fm., Kissenger Lst. Mbr.						
14-1						
Propora thebesensis (n = 10)	2 (20%)	3 (30%)	2 (20%)	1 (10%)	2 (20%)	0 (0%)
		7 (70%)			3 (30%)	
Paleofavosites subelongus (n = 24)	2 (8%)	7 (29%)	3 (13%)	0 (0%)	6 (25%)	6 (25%)
		12 (50%)			12 (50%)	
15-1						
Propora thebesensis (n = 4)	0 (0%)	3 (75%)	0 (0%)	0 (0%)	1 (25%)	0 (0%)
		3 (75%)			1 (25%)	
Paleofavosites subelongus (n = 4)	0 (0%)	2 (50%)	1 (25%)	0 (0%)	0 (0%)	1 (25%)
		3 (75%)			1 (25%)	
Mosalem Fm., coral-rich bedding surface						
32-1z						
Paleofavosites subelongus (n = 23)	0 (0%)	2 (9%)	1 (4%)	1 (4%)	11 (48%)	8 (35%)
		3 (13%)			20 (87%)	

[1] Includes two parts of one composite corallum that are considered separately.

umet), in which both species occur, indicate that *P. subelongus* was more likely to develop low domical forms than was *P. thebesensis.* This corresponds with observed differences in basal astogeny. Corallites tended to diverge widely from the point of initiation in *P. subelongus,* producing flatter corallum bases (Pl. 16, fig. 5), whereas corallites of *P. thebesensis* diverged less broadly and corallum bases are usually more conical (Pl. 3, figs. 4, 8). It is because of these interspecific differences that comparisons of growth form distribution between collection intervals are made within species.

There are substantial differences in growth form among stratigraphic units (Text-fig. 10; Table 6). Domical coralla of *Propora thebesensis* having relatively flat basal surfaces (*i.e.,* M $\ll$ 0.5H) are dominant in the *Brevilamnulella* beds of the Keel Formation at Section 23 (Lawrence Quarry). In the Kissenger Limestone Member of the Bryant Knob Formation at Section 14 (Higginbotham Farm) and Section 15 (Calumet), coralla of *P. thebesensis* are domical or bulbous and plot near the boundary between those categories (*i.e.,* M nearly 0.5H). Bulbo-columnar specimens of *P. thebesensis,* some with steeply conical bases (*i.e.,* M $\gg$ 0.5H), are dominant in the Leemon Formation at Section 31 (Thebes North). In *Paleofavosites subelongus,* domical coralla having somewhat conical bases (*i.e.,* M approaching 0.5H) are dominant on the coral-rich bedding surface of the Mosalem Formation at Section 32 (Thomson East). Domical and bulbous forms are common for *P. subelongus* from Sections 14 and 15.

Within a species, variation in shapes of corallum bases may reflect differences in sedimentation rate and/or sediment firmness during growth (see Philcox, 1971, p. 340; Gibson and Broadhead, 1989, pp. 294–295). If sediment did not accumulate around a corallum, and if it was sufficiently firm to provide a stable substrate that prevented subsidence as weight of the skeleton increased during growth, then a flat basal surface would have developed during colony expansion over a level bottom. The greater the rate of sediment accumulation and/or corallum subsidence, the more steeply conical the base would become (*i.e.,* the greater the M:H ratio, other things being equal). The proportions of domical and bulbous coralla of a species may therefore reflect the sedimentation rate and substrate stability.

Table 7.—Growth forms and spacing of tabulae and dissepiments (where applicable) in selected tabulate coralla from the Edgewood Province. *High* = high bulbous and/or high domical, *low* = low bulbous and/or low domical, *n* = number of coralla, range and standard deviation (*s.d.*) are for corallum means.

species	*growth forms*				*no. of tabulae in 5 mm*				*no. of dissepiments in 5 mm*			
units *section-intervals*	*columnar*	*high*	*low*	*n*	*mean*	*range*	*s.d.*	*n*	*mean*	*range*	*s.d.*	*n*
Propora thebesensis												
Keel Fm., *Brevilamnulella* beds												
23-2	0 (0%)	3 (50%)	3 (50%)	4	9.2	6.2–13.3	2.0	10	17.5	11.9–20.0	3.8	4
Leemon Fm.												
31-1 and 31-1b	7 (70%)	1 (10%)	2 (20%)	10[1]	6.7	4.4–8.2	1.1	12	13.0	10.6–17.0	2.3	6
Bryant Knob Fm., Kissenger Lst. Mbr.												
14-1	3 (30%)	5 (50%)	2 (20%)	10	7.1	5.0–11.2	1.7	18	13.9	11.4–15.8	1.4	11
15-1	0 (0%)	4 (100%)	0 (0%)	4	7.9	4.6–9.6	1.6	11	14.0	12.8–14.9	0.9	4
Paleofavosites subelongus												
Leemon Fm.												
31-1 and 31-1b	0 (0%)	0 (0%)	1 (100%)	1	3.8	3.1–4.8	0.8	4	—	—	—	—
Bryant Knob Fm., Kissenger Lst. Mbr.												
14-1	2 (8%)	13 (54%)	9 (38%)	24	4.8	2.8–6.7	1.1	32	—	—	—	—
15-1	0 (0%)	2 (50%)	2 (50%)	4	5.8	3.5–10.9	2.6	6	—	—	—	—
Mosalem Fm., coral-rich bedding surface												
32-1z	1 (4%)	13 (57%)	9 (39%)	23	3.7	2.5–5.8	0.7	17	—	—	—	—

[1] Includes two parts of one composite corallum that are considered separately.

Another aspect of corallum form that may reflect sedimentation rate and/or substrate stability is the height : width ratio. Tall colonies are thought to shed sediment more readily than lower ones (*e.g.*, Manten, 1971, p. 431; Pandolfi, 1984, p. 540; Young and Scrutton, 1991, pp. 380, 381), although form must have combined with polyp morphology and behavior to keep surfaces sediment-free (Hubbard and Pocock, 1972; Bak and Elgershuizen, 1976; Lasker, 1980). Colony growth may have been directed preferentially upward in order to compensate for sediment accumulation (see Young and Scrutton, 1991, p. 381) or corallum subsidence. The greater the rate of sediment accumulation and/or corallum subsidence, the higher the height:width ratio would have become (other things being equal). The proportions of low, high, and columnar coralla may therefore reflect the sedimentation rate and substrate stability.

A high overall frequency of low domical forms of *Propora thebesensis* occurs in the *Brevilamnulella* beds (Text-fig. 10; Tables 6, 7), suggesting a stable substrate and low sedimentation rate. This is consistent with interpretations based on the presence of aligned shells in the sediment, the absence of composite coralla, and the high proportions of encrusted and encrusting colonial coralla. The occurrence of taller domical and bulbous forms of *P. thebesensis* in the Kissenger Limestone at Section 14 (Higginbotham Farm) and Section 15 (Calumet) suggests that the substrates were less stable and/or that sedimentation rates were higher. It is more likely that the latter was the case, since the low proportion of encrusted coralla and absence of encrusting coralla are consistent with the interpretation that sedimentation rates were high, and aligned clasts in the sediment at Section 14 and the low proportion of composite coralla suggest stable substrates. The predominantly bulbo-columnar coralla of *P. thebesensis* in the Leemon Formation at Section 31 (Thebes North) suggest a high sedimentation rate and/or unstable substrate. That both factors were involved is indicated by the well-rounded grains comprising the sediment, the high proportion of composite coralla, low proportion of encrusted coralla, and absence of encrusting coralla.

For *Paleofavosites subelongus*, the highest frequency of domical coralla is observed on the coral-rich bedding surface of the Mosalem Formation (Text-fig. 10; Table 6). The inference that the substrate was stable is consistent with the high sediment cohesion suggested by the mudstone to wackestone lithology and absence of composite coralla. The inferred low sedimentation rate is consistent with the interpretation that a break in sedimentation permitted colonization of the bedding surface by numerous corals. The proportions of domical and bulbous coralla of *P. subelongus* on the coral-rich bedding surface of the Mosalem differ significantly from those in the Kissenger Limestone at Section 14 (Higginbotham Farm) ($\chi^2 = 5.779$; $\chi^2_{0.05} = 3.841$, 1 d.f.). The greater frequency of bulbous coralla in the Kissenger at Section 14 and Section 15 (Calumet) is consistent with higher sedimentation rates, as discussed for *Propora thebesensis,* above.

There may be a genetic component to differences in growth form within both *Propora thebesensis* and *Paleofavosites subelongus* among the collections studied. At least some of the stratigraphic units differ slightly in age, the localities are separated by considerable distances, and internal morphology can be distinctly different between section-intervals (see *Aspects of Intraspecific Variation,* pp. 35, 39). There is a strong correlation between genotype and growth form in some modern corals (*e.g.,* Hunter, 1985; Willis and Ayre, 1985). It is probable, however, that environmental factors were more significant in determining the observed variation; the corals in these collections clearly lived under quite different environmental conditions. Sedimentation rate and substrate stability appear to have been important factors controlling the expressed forms of Edgewood colonial coralla, a conclusion also reached in studies of some other heliolitids and favositids (*e.g.,* Manten, 1971, pp. 431, 432; Philcox, 1971; Pandolfi, 1984; Gibson and Broadhead, 1989; Young and Scrutton, 1991).

GROWTH RATE

Absolute linear growth rates of Paleozoic corals are generally inferred using the widely accepted technique of measuring thicknesses of presumably annual high- and low-density couplets within the skeleton (see Scrutton, 1989, p. 37). Cyclic growth banding such as this is very subtle to unrecognizable in Edgewood colonial coralla, so we are unable to use this technique to determine growth rates. There is some evidence from tabulate corals that horizontal skeletal elements were formed at relatively uniform time intervals within corallites of a corallum and within coralla of a species, regardless of growth rate and colony form (Scrutton, 1989, p. 38; Young and Scrutton, 1991, p. 377). Comparisons of mean tabular or dissepimental spacing may therefore reveal differences in relative linear growth rates. This method yields meaningful results in our analysis of Edgewood corals; inferred relative linear growth rates can be related to environmental factors such as sedimentation rate, substrate stability, and turbidity.

As a measure of tabular or dissepimental spacing, we use the mean number of horizontal skeletal elements per 5 mm vertical interval within a corallum (see *Biometric Methods,* p. 44). The overall mean of corallum means is calculated for specimens of *Propora thebesensis* and *Paleofavosites subelongus* in collections from the Edgewood Province for which sufficient data are available to permit comparison (Table 7). Overall mean values for tabulae as well as dissepiments in *P. thebesensis* and for tabulae in *P. subelongus* increase from the Leemon Formation at Section 31 (Thebes North) to the Kissenger Limestone Member of the Bryant Knob Formation at Section 14 (Higginbotham Farm) to the Kissenger at Section 15 (Calumet). Although there is considerable variability of corallum means within each collection, the consistent relationship when comparing overall means for these collections suggests that this pattern is real; thus, the two species may have responded in the same way to environmental differences among the localities. The highest values for *P. thebesensis* occur in the *Brevilamnulella* beds of the Keel Formation at Section 23 (Lawrence Quarry). The lowest values for *P. subelongus* are recorded from the coral-rich bedding surface in the Mosalem Formation at Section 32 (Thomson East).

Inferred relative linear growth rates of coralla are inversely proportional to values for spacing of tabulae or dissepiments (*e.g.,* a low growth rate would result in crowding of horizontal skeletal elements, giving a high value for spacing). Thus, mean coral growth rates increased from lowest in the *Brevilamnulella* beds, to the Kissenger Limestone at Section 15 (Calumet), to the Kissenger at Section 14 (Higginbotham Farm), to the Leemon Formation, to highest on the coral-rich bedding surface in the Mosalem.

In *Propora thebesensis,* growth rates correlate closely with the height : width aspect of growth form, suggesting that the two are interrelated. The collection from the *Brevilamnulella* beds at Section 23 (Lawrence Quarry) has the lowest mean growth rate and the greatest proportion of low growth forms (Table 7). The highest mean growth rate for this species is in the Leemon Formation at Section 31 (Thebes North), where the proportion of columnar forms is greatest. Growth rates in the Kissenger Limestone at Section 14 (Higginbotham Farm) and Section 15 (Calumet) are intermediate, and the distributions of growth forms are centered on the "high" category. We have related the corallum height : width ratio to sedimentation rate and substrate stability, and it follows that growth rate may also be an indicator of those environmental parameters. A greater vertical growth rate would have helped to maintain the position of the living polypal colony surface above the substrate where sedimentation and/or corallum subsidence rates were high. We recognize that other factors would also have been involved in determining growth rates; controls over coral growth are complex and in general poorly understood (see Buddemeier and Kinzie, 1976).

It is noteworthy that a similar close relationship involving growth rate, height : width aspect of growth form, and sedimentation rate has been found in another heliolitid, *Stelliporella parvistella* (Roemer) from the Silurian of northwestern Europe. Young and Scrutton (1991, pp. 377, 380, 381) concluded that growth rates in that species were greater in columnar and branching colonies, the predominant forms where sedimentation was moderate, than in tabular and domical colonies, which were dominant where sedimentation was minimal. It was found by Young and Scrutton that growth rates and forms could change within a colony in response to changes in sedimentation rate. In the Edgewood favositid *Paleofavosites subelongus,* there does not appear to be a consistent correlation between growth rate and the height : width aspect of growth form (Table 7).

The low mean growth rate inferred for corals in the *Brevilamnulella* beds suggests a low sedimentation rate and stable substrate. That is consistent with interpretations based on the presence of aligned brachiopod shells in the sediment, the absence of composite coralla, the high proportions of encrusted and encrusting colonial coralla, the high frequency of domical growth forms, and the high proportion of low forms among the domical and bulbous coralla. Higher mean growth rates for corals in the Kissenger Limestone are consistent with the interpretation that the sedimentation rate was higher, based on the low proportion of encrusted coralla, absence of encrusting coralla, dominance of bulbous coralla, and greater proportion of high and columnar forms. High mean growth rates for corals in the Leemon Formation suggest that the sedimentation rate was high and/or the substrate was unstable. The conclusion that both factors were involved is consistent with interpretations based on the roundness of grains comprising the sediment, the high proportion of composite coralla, low proportion of encrusted coralla, absence of encrusting coralla, and dominance of bulbous and columnar growth forms.

The high mean growth rate inferred for colonies on the coral-rich bedding surface in the Mosalem Formation is more difficult to interpret. It does not appear to reflect a high sedimentation rate or a substrate that was unstable. The predominance of domical coralla and high proportion of low growth forms suggest that the sedimentation rate was low and the substrate was stable. A low sedimentation rate is consistent with the interpretation that this bed represents a break in deposition. The conclusion that the substrate was stable is supported by the mudstone to wackestone lithology, suggesting high sediment cohesion, and the absence of composite coralla. Growth rates of modern corals decrease as turbidity increases (see Buddemeier and Kinzie, 1976, p. 211). Comparatively low growth rates might therefore be expected for the coral-rich bedding surface in the Mosalem, where the lithology, low proportion of coralla with encrusters, and absence of encrusting coralla are considered to reflect relatively high turbidity. In this case, it is possible that the high growth rate was related to favorable environmental conditions that permitted colonization of the bedding surface by numerous corals (*e.g.,* factors such as temperature, nutrients).

CORALLUM SIZE

Our study of Edgewood colonial corals shows that the sizes attained by coralla may reflect environmental factors such as substrate stability and sedimentation rate. The size distribution of coralla on a bed may provide information on population structure and history. As measures of size, we calculate the average linear dimensions of Edgewood colonial coralla (*i.e.,* (maximum width + height) ÷ 2). The common use of basal diameter alone to represent size may bias results because it will inflate values for specimens with low growth forms relative to those with taller forms. Comparisons of size data are made within species; possible differences in growth rates among species would affect size distributions. Sufficient data for comparisons at different localities were obtained from two massive tabulate species (Table 8).

The average and maximum sizes of *Propora thebesensis* are much greater in the *Brevilamnulella* beds of the Keel Formation at Section 23 (Lawrence Quarry) than in the Leemon Formation at Section 31 (Thebes North) and the Kissenger Limestone Member of the Bryant Knob Formation at Section 14 (Higginbotham Farm) and Section 15 (Calumet) (Table 8). This is especially noteworthy considering that the inferred mean linear growth rate for this species is lower in the *Brevilamnulella* beds than in the other units. The observed size distributions are not likely to have resulted from mechanical sorting; at each of these localities the degree of variability of corallum size is quite large, and very small specimens are present. The attainment of large sizes by corals in the *Brevilamnulella* beds is considered to reflect environmental stability over relatively long periods of time. This is consistent with interpretations of high substrate stability and low sedimentation rate based on the absence of composite coralla, the numerous encrusting relationships, the high proportion of low domical corallum forms, and the low mean growth rate of *P. thebesensis.*

Coralla of *Paleofavosites subelongus* have similar average sizes in the Kissenger Limestone Member of the

Table 8.—Sizes of massive tabulate coralla in selected units within the Edgewood Province. *s.d.* = standard deviation, *c.v.* = coefficient of variation.

species *units* *section-intervals (n = no. of coralla)*	*average linear dimensions* *mean*	 *range*	 *s.d.*	 *c.v.*
Propora thebesensis				
Keel Fm., *Brevilamnulella* beds 23-2 (n = 6)	52.8 mm	16.5–103.0 mm	35.5 mm	67.2
Leemon Fm. 31-1 and 31-1b (n = 10)	34.8 mm	14.5–65.5 mm	18.3 mm	52.6
Bryant Knob Fm. Kissenger Lst. Mbr. 14-1 and 15-1 (n = 14)	30.9 mm	12.5–52.5 mm	12.8 mm	41.4
Paleofavosites subelongus				
Bryant Knob Fm., Kissenger Lst. Mbr. 14-1 and 15-1 (n = 28)	34.4 mm	11.5–67.5 mm	13.8 mm	40.1
Mosalem Fm., coral-rich bedding surface 32-1z (n = 23)	39.5 mm	22.5–56.5 mm	8.8 mm	22.3

Bryant Knob Formation at Section 14 (Higginbotham Farm) and Section 15 (Calumet), and on the coral-rich bedding surface of the Mosalem Formation at Section 32 (Thomson East) (Table 8). At Section 32, however, there is considerably less variability in size, and small coralla with average linear dimensions less than 22.5 mm are absent. This is not likely to have resulted from mechanical sorting; a higher proportion of coralla are in growth orientation and the frequency of abraded specimens is far lower at Section 32 than elsewhere in the Edgewood Province, suggesting comparatively low energy conditions. Perhaps this bedding surface was colonized by an influx of larvae during a very short period of time, and the resulting population was later buried during a single event involving relatively little disturbance of the coralla. Unfortunately, poor preservation of the corallum bases prevents us from determining whether the colonies originated from sexually produced larvae or as a result of asexual fragmentation (see Lee and Noble, 1990).

PALEOENVIRONMENTS

Here we examine the general environments inhabited by Edgewood colonial corals, based on the lithologies in which they occur. Environmental preferences and tolerances are shown to vary among taxa. A diversity gradient is recognized within the Edgewood Province, and is related to an environmental gradient. We are able to make detailed paleoenvironmental determinations, based on comparative taphonomy and paleoecology of colonial corals, for selected stratigraphic units and localities.

A wide spectrum of shallow marine depositional environments is represented by latest Ordovician to earliest Silurian strata in the Edgewood Province (see Text-figs. 2–7). Edgewood colonial corals are typically absent or rare in units considered to represent restricted-marine, low-energy environments. They do not occur in the Wilhelmi Formation at Section 3 (Garden Prairie), where evaporite crystal molds are present in dolomitized mudstone. In general, colonial corals are absent or rare in argillaceous, dolomitized mudstone to wackestone of the Wilhelmi in northeastern Illinois and the Mosalem Formation of northwestern Illinois and eastern Iowa. Exceptions are as follows: the Wilhelmi at Section 37 (Essex), where *Halysites alexandricus, Paleofavosites subelongus,* and *Aulopora* sp. A are present (*H. alexandricus* is common); the coral-rich bedding surface in the Mosalem at Section 32 (Thomson East), where *Propora thebesensis, H. alexandricus,* and *P. subelongus* occur (*P. subelongus* is abundant); and the channel-fill beds in the Mosalem at Section 32, where *Pycnostylus* sp. A is abundant.

Colonial corals are absent or uncommon in other fine-grained or argillaceous units that suggest turbid environments. They have not been found in the "laminated calcilutite unit" of the Keel Formation at Section 24 (Coal Creek), or in shaly beds of the lower Leemon Formation at Section 31 (Thebes North) and the entire Leemon at Section 19 (New Wells). *Paleofavosites subelongus* is rare in dolomitic wackestone of the Cyrene Formation at Section 13 (Bowling Green), and uncommon in argillaceous, dolomitic packstone comprising the unnamed member of the Bryant Knob Formation at Section 18 (Kissenger). Of the Edgewood colonial corals, *P. subelongus* may have been the most tolerant of turbid conditions.

Colonial corals are typically absent or rare in units considered to represent open-marine conditions with the highest energy levels and unstable, shifting substrates. We did not find them in cross-bedded oölites at the base of the Leemon Formation at Section 20

(Short Farm) or in the Noix oölite of west-central Illinois and northeastern Missouri, although *Halysites* has been reported as rare in blocks thought to be from the Noix (Amsden, 1974, fig. 9). Colonial corals are generally absent or rare in oölites of the Keel Formation in south-central Oklahoma. Single specimens of *Halysites alexandricus* were collected at Section 24 (Coal Creek) and Section 25 (Hunton). In the Keel oölite at Section 23 (Lawrence Quarry), however, *Propora thebesensis, Propora savagei, H. alexandricus, Paleofavosites subelongus,* and *Palaeophyllum* sp. are present (*H. alexandricus* is common). A single specimen of *H. alexandricus* is known from a silicified oölite at the top of the Cason Shale at Section 33 (Buffalo River). Of the Edgewood colonial corals, it appears that *H. alexandricus* was most tolerant of very high energy levels and shifting substrates. This is consistent with the conclusion that cateniform growth was advantageous in such environments (Lee and Elias, 1991).

Edgewood colonial corals are typically found in bioclastic packstones to grainstones, some of which are oölitic. These units are considered to represent open-marine, high-energy environments. They contain the most diverse colonial coral associations in the Edgewood Province. Examples are as follows: the *Brevilamnulella* beds of the Keel Formation at Section 23 (Lawrence Quarry), where six species were found (*Propora thebesensis, Halysites alexandricus,* and *Catenipora lawrencica* are common); the upper Leemon Formation at Section 31 (Thebes North), where seven species are known (*P. thebesensis* is common); and the Kissenger Limestone Member of the Bryant Knob Formation at Section 14 (Higginbotham Farm), where six species occur (*Paleofavosites subelongus* is abundant, *P. thebesensis* is common).

There appears to be a diversity gradient within the Edgewood Province. Eight species of colonial corals representing the Edgewood Assemblage are known from south-central Oklahoma, seven occur in southern Illinois and southeastern Missouri and in northeastern Missouri, and four are present in northeastern Illinois and in northwestern Illinois (Table 1). Western north-central Arkansas is excluded from this analysis because data for that area are based on limited sampling at only one stratigraphic section. The northward decrease in diversity is considered to reflect an environmental gradient from the most open, normal-marine conditions nearest the continental margin in the south, to increasingly restricted conditions farther north into the cratonic interior (see also McAuley and Elias, 1990, p. 27).

Detailed environmental determinations are possible using comparative taphonomy and paleoecology, as discussed above (pp. 22–33). A synthesis of environmental indicators and interpretations for five localities from which sufficient data are available is presented in Table 9. The different lines of evidence provide consistent results at each locality, and permit recognition of subtle as well as major differences in environmental conditions among the stratigraphic units.

The Kissenger Limestone Member of the Bryant Knob Formation at Section 14 (Higginbotham Farm) and Section 15 (Calumet) was deposited in high-energy conditions. Differences in the degree of corallum abrasion suggest that energy levels were slightly lower for the *Brevilamnulella* beds of the Keel Formation at Section 23 (Lawrence Quarry), and highest for the upper Leemon Formation at Section 31 (Thebes North). The coral-rich bedding surface in the Mosalem Formation at Section 32 (Thomson East) was deposited in low- to perhaps moderate-energy conditions.

Substrate stability was high during deposition of the Kissenger Limestone in the Bryant Knob Formation and the coral-rich bedding surface in the Mosalem Formation; numerous lines of evidence suggest that it was even higher for the *Brevilamnulella* beds in the Keel Formation. Substrate stability in the Leemon Formation was low. Turbidity was relatively high only in the case of the coral-rich bedding surface. The sedimentation rate was highest for the Leemon and moderate to high for the Kissenger. The *Brevilamnulella* beds and the coral-rich bedding surface were characterized by low sedimentation rates, with numerous lines of evidence suggesting the lowest rate for the *Brevilamnulella* beds.

ASPECTS OF INTRASPECIFIC VARIATION

INTRODUCTION

The quantity of numerical data collected in our study for the definition and description of coral species permits the observation of trends in variation that would not otherwise be recognized. This section begins with a synthesis of certain aspects of variation within species. This provides a basis for the subsequent comparison of patterns of variation among the more common species and orders. General patterns of intracolony, intraspecies, and interspecies variation in Paleozoic colonial corals are, as yet, poorly understood. As described in reviews by Oliver (1968) and Scrutton (1989), many studies have examined aspects of variation within single species or taxonomic groups (*e.g.*, Philip, 1960; Tesakov, 1973; Dixon, 1974; Scrutton and Powell, 1980; Scrutton, 1983, 1990; Bondarenko, 1985; Young and Noble, 1989; Hubmann, 1992). Our study differs from these by examining intracorallum, intralocality, and interlocality variation of all colonial species occurring in a particular stratigraphic interval throughout a large geographic area.

An examination of colonial coral variation must consider several factors. These include ontogeny (development of an individual polyp, as recorded in the corallite), astogeny (development of the colony, as recorded in the corallum), cyclomorphic patterns (periodic morphologic changes recorded by density banding in the corallum), and topomorphic patterns (morphologic differences in different areas of the colony surface, recorded on and in the corallum). Environmental and genetic differences between populations must also be considered. In our analysis we have focused on those structural or design constraints within coralla that resulted in correspondences between numerically analyzed morphologic characters, and on determination of the limits of intraspecific variation within the various groups. Through this methodology, a valid approach to the recognition and definition of colonial coral species may be developed.

VARIATION IN INDIVIDUAL SPECIES

In the following paragraphs, we present an overview of patterns of variation within individual species. The details are documented and illustrated in *Systematic Paleontology*. Variation in numerical characters is described under *Intraspecific variation* for each species. Non-numerical aspects of intraspecific variability are considered under *Description of coralla, Astogeny and corallite increase,* and *Microstructure* for each species.

Propora thebesensis.—Analysis of variation allows us to correlate several morphologic characters. Variation in internal morphology can be related to both geographic locality and growth form.

We have previously analyzed the relationship between size and spacing of tabularia in this species (Young and Elias, 1993). It was demonstrated that an unusually high variability of tabularium diameter within a corallum is commonly related to the density of spacing of tabularia, and is thus partly controlled by structural factors. Many specimens show little variability in tabularium diameter, and have strongly unimodal frequency distributions for this character. Such distributions are similar to those for coralla of many other heliolitid species (Young and Elias, 1993, fig. 2). These strongly unimodal distributions tend to be associated with coralla having more widely spaced tabularia. In coralla with dense tabularium spacing, a larger number of small individuals may have resulted from slower tabularium expansion rates where walls were in contact (Young and Elias, 1993, fig. 5). This yields a broader unimodal or bimodal distribution. The smaller mode of a bimodal distribution probably represents a burst of corallite increase (budding).

As shown above, intracorallum variability of tabularium diameters is related to structural aspects of corallite packing and cyclomorphic patterns. This variability also shows some correlation with locality (see *Intraspecific variation,* pp. 49, 50). Interlocality differences suggest that genetic and/or environmental factors played a role in tabularium size and spacing, and consequently also in the tabularium size-frequency distributions.

There is a strong positive correlation between mean tabularium area and mean corallite area on transverse sections (see *Intraspecific variation,* p. 50). This is similar to the pattern observed in many other heliolitid species (see Young and Noble, 1990a, fig. 3; 1990b, fig. 2).

Variation in these internal characters may be related to corallum growth form. Taller growth forms are most abundant at those localities where tabularia are more densely spaced, such as Section-intervals 31-1 and 31-1b (Thebes North), and Section-interval 14-1 (Higginbotham Farm). Lower forms are most common where tabularia are broadly spaced, as in Section-interval 23-2 (Lawrence Quarry). Taller growth forms also tend to be associated with wider vertical spacing of tabulae and dissepiments (see *Growth Rate,* p. 31). The presence of such relationships may indicate that internal morphology was more strongly tied to environment than is commonly accepted, but it also suggests that growth forms in a single species could have varied due to genotypic differences between populations.

Tabulations of morphologic characters at the major localities (Tables 10, 11) illustrate the close similarities between specimens from most places, but also show that coralla from Section-interval 23-2 tend to lie at one end of the spectrum of variation. The lower growth forms, widely spaced crenulate tabularia, thick walls, well developed septa, and more closely spaced horizontal elements that are typical of this locality may have developed as a response to the distinct environmental conditions prevalent there (see *Growth Form,* pp. 29, 30; *Paleoenvironments,* p. 34). It is also possible, however, that the geographic distance between Section 23 (Lawrence Quarry) and the other major localities may have permitted a degree of reproductive isolation, resulting in significant genotypic differences.

Propora savagei.—Aspects of intraspecific variation analyzed here show patterns typical of the Proporidae. These include the unimodal frequency distribution for tabularium diameter within a corallum and the positive correlation between tabularium area and corallite area (see *Intraspecific variation,* p. 57). The frequency distribution has a slight negative skewness. This was probably caused by a low rate of corallite increase.

Significant variation between localities is observed

Table 9.—Environmental interpretations for selected units within the Edgewood Province, based on lithologies and characteristics of colonial corals including *Propora thebesensis* and *Paleofavosites subelongus.* × indicates an environmental interpretation (for explanations, see *The Edgewood Colonial Corals,* pp. 22–34).

	energy level					*substrate stability*			*turbidity*	*sedimentation rate*					
units *section-intervals* *environmental indicators*	*highest*	*high*	*moderately high*	*moderate*	*low*	*highest*	*high*	*low*	*relatively high*	*highest*	*high*	*moderately high*	*moderate*	*low*	*lowest*
Keel Fm., *Brevilamnulella* beds															
23-2															
lithology: oölitic, bioclastic packstone–grainstone; aligned shells	—	×	—	—	—	—	×	—	—	—	—	—	—	—	—
proportion abraded (massive tabulate coralla): high	—	×	—	—	—	—	—	—	—	—	—	—	—	—	—
degree of abrasion (massive tabulate coralla): moderately high	—	—	×	—	—	—	—	—	—	—	—	—	—	—	—
proportion overturned (massive tabulate coralla): high	—	×	—	—	—	—	—	—	—	—	—	—	—	—	—
proportion noncomposite (tabulate coralla): high	—	—	—	—	—	—	×	—	—	—	—	—	—	—	—
proportion of colonial coralla with encrusters: highest	—	—	—	—	—	×	—	—	—	—	—	—	—	—	×
proportion of colonial coralla that are encrusters: highest	—	—	—	—	—	×	—	—	—	—	—	—	—	—	×
proportion of domical growth forms (*P. thebesensis*): highest	—	—	—	—	—	×	—	—	—	—	—	—	—	—	×
proportion of domical forms with flat bases (*P. thebesensis*): highest	—	—	—	—	—	×	—	—	—	—	—	—	—	—	×
proportion of low growth forms (*P. thebesensis*): highest	—	—	—	—	—	×	—	—	—	—	—	—	—	—	×
inferred mean growth rate (*P. thebesensis*): lowest	—	—	—	—	—	×	—	—	—	—	—	—	—	—	×
average and maximum corallum size (*P. thebesensis*): highest	—	—	—	—	—	×	—	—	—	—	—	—	—	—	×
Leemon Fm.															
31-1 and 31-1b															
lithology: skeletal grainstone; moderately well-rounded grains	—	×	—	—	—	—	—	×	—	—	—	—	—	—	—
proportion abraded (massive tabulate coralla): high	—	×	—	—	—	—	—	—	—	—	—	—	—	—	—
degree of abrasion (massive tabulate coralla): highest	×	—	—	—	—	—	—	—	—	—	—	—	—	—	—
proportion noncomposite (tabulate coralla): lowest	—	—	—	—	—	—	—	×	—	—	—	—	—	—	—
proportion of colonial coralla with encrusters: low	—	—	—	—	—	—	—	×	—	—	×	—	—	—	—
proportion of colonial coralla that are encrusters: none	—	—	—	—	—	—	—	×	—	—	×	—	—	—	—
proportion of domical growth forms (*P. thebesensis*): lowest	—	—	—	—	—	—	—	×	—	×	—	—	—	—	—
proportion of columnar growth forms (*P. thebesensis*): highest	—	—	—	—	—	—	—	×	—	×	—	—	—	—	—
inferred mean growth rate (*P. thebesensis* and *P. subelongus*): high	—	—	—	—	—	—	—	×	—	—	×	—	—	—	—
Bryant Knob Fm., Kissenger Lst. Mbr.															
14-1 and 14-2															
lithology: fossiliferous grainstone; aligned clasts	—	×	—	—	—	—	×	—	—	—	—	—	—	—	—
proportion abraded (massive tabulate coralla): high	—	×	—	—	—	—	—	—	—	—	—	—	—	—	—
degree of abrasion (massive tabulate coralla): high	—	×	—	—	—	—	—	—	—	—	—	—	—	—	—

Table 9.—Continued.

	energy level					substrate stability			turbidity	sedimentation rate					
units section-intervals environmental indicators	highest	high	moderately high	moderate	low	highest	high	low	relatively high	highest	high	moderately high	moderate	low	lowest
proportion overturned (massive tabulate coralla): high	—	×	—	—	—	—	—	—	—	—	—	—	—	—	—
proportion noncomposite (tabulate coralla): high	—	—	—	—	—	—	×	—	—	—	—	—	—	—	—
proportion of colonial coralla with encrusters: moderately low	—	—	—	—	—	—	—	—	—	—	—	×	—	—	—
proportion of colonial coralla that are encrusters: none	—	—	—	—	—	—	—	—	—	—	×	—	—	—	—
proportion of domical growth forms (*P. thebesensis* and *P. subelongus*): moderate	—	—	—	—	—	—	—	—	—	—	—	—	×	—	—
proportion of columnar growth forms (*P. thebesensis*): moderate	—	—	—	—	—	—	—	—	—	—	—	×	—	—	—
inferred mean growth rate (*P. thebesensis* and *P. subelongus*): moderate	—	—	—	—	—	—	—	—	—	—	—	—	×	—	—
15-1															
lithology: grainstone	—	×	—	—	—	—	—	—	—	—	—	—	—	—	—
proportion abraded (massive tabulate coralla): high	—	×	—	—	—	—	—	—	—	—	—	—	—	—	—
degree of abrasion (massive tabulate coralla): high	—	×	—	—	—	—	—	—	—	—	—	—	—	—	—
proportion noncomposite (tabulate coralla): high	—	—	—	—	—	—	×	—	—	—	—	—	—	—	—
proportion of colonial coralla with encrusters: moderately low	—	—	—	—	—	—	—	—	—	—	—	×	—	—	—
proportion of colonial coralla that are encrusters: none	—	—	—	—	—	—	—	—	—	—	×	—	—	—	—
proportion of domical growth forms (*P. thebesensis* and *P. subelongus*): low	—	—	—	—	—	—	—	—	—	—	×	—	—	—	—
proportion of high growth forms (*P. thebesensis*): highest	—	—	—	—	—	—	—	—	—	—	—	—	×	—	—
inferred mean growth rate (*P. thebesensis* and *P. subelongus*): moderate	—	—	—	—	—	—	—	—	—	—	—	—	×	—	—
Mosalem Fm., coral-rich bedding surface															
32-1z															
lithology: mudstone–wackestone	—	—	—	—	×	—	×	—	×	—	—	—	—	—	—
proportion abraded (massive tabulate coralla): low	—	—	—	—	×	—	—	—	—	—	—	—	—	—	—
degree of abrasion (massive tabulate coralla): low	—	—	—	—	×	—	—	—	—	—	—	—	—	—	—
proportion overturned (massive tabulate coralla): moderate	—	—	—	×	—	—	—	—	—	—	—	—	—	—	—
proportion noncomposite (tabulate coralla): high	—	—	—	—	—	—	×	—	—	—	—	—	—	—	—
proportion of colonial coralla with encrusters: low	—	—	—	—	—	—	—	—	×	—	—	—	—	—	—
proportion of colonial coralla that are encrusters: none	—	—	—	—	—	—	—	—	×	—	—	—	—	—	—
proportion of domical growth forms (*P. subelongus*): highest	—	—	—	—	—	×	—	—	—	—	—	—	—	—	×
proportion of domical forms with flat bases (*P. subelongus*): low	—	—	—	—	—	—	×	—	—	—	—	—	—	×	—

Table 10.—Interlocality variation in qualitatively defined morphologic characters of *Propora thebesensis* in the east-central United States. P = predominant, C = common, R = rare or weakly developed, A = absent.

	sections/section-intervals						
characters	*23-2*	*31-1 and 31-1b*	*14-1*	*15-1*	*16*	*18*	*32-1c*
columnar forms	A	P	C	A	—	—	—
high bulbous and domical forms	C	C	C	P	—	—	—
low bulbous and domical forms	C	C	R	A	—	—	—
smooth-walled tabularia	R	P	P	C	R	—	C
crenulate tabularia	P	R	C	C	P	—	R
subpolygonal tabularia	R	C	C	C	C	P	R
cyclomorphic thickening	C	R	R	R	—	—	—

in comparisons of coralla from Section 20 (Short Farm) with those from the other localities. These differences may have evolutionary significance, and are considered in detail elsewhere (see *Discussion,* p. 58).

Propora speciosa.—Coralla are very consistent in numerically analyzed characters, but differ visibly in patterns of thickening of skeletal elements. These patterns are not correlated with interlocality variability; some of the greatest differences occur between specimens from the same locality (see *e.g.,* Pl. 7, figs. 1, 7). The corallum from the upper Mosalem Formation at Section 32 (Thomson East) (see Pl. 7, fig. 8) is younger than and is separated by a considerable geographic distance from the specimens from Section 31 (Thebes North) and the Gale Section. Nevertheless, it is similar to them and its numerical characters are mostly close to the species means (see *Description of coralla,* p. 59; *Discussion,* p. 61).

A relatively low degree of variability is observed in specimens of *Propora speciosa* from the east-central United States. This is consistent with the character of this species as noted by Dixon (1974, pp. 581, 582) in his discussion of material from the Ellis Bay Formation on Anticosti Island, Québec, and also as commented on by Scrutton (1989, p. 40) (see also *Comparisons of Species,* p. 42).

Halysites alexandricus.—Although this species is common in the study region, variation between localities is not distinct. This observation may be related to preservational problems, since the fragmentary nature of much material limits numerical analysis.

Paleofavosites subelongus.—This species shows a high degree of variability in several important morphologic characters. It is like other favositids (see Scrutton, 1989, pp. 40, 41; Lee and Noble, 1988, p. 38) in often exhibiting extreme variation in intracorallum corallite size. Mean corallite sizes can also be quite different between coralla. Since this parameter is commonly used to discriminate species, we document this variability and examine possible controls of corallite size. Other characters of *Paleofavosites subelongus* that show interesting types of variation include growth form, initial corallum astogeny, and the degree of development or thickening of skeletal characters.

Corallite size-frequency distributions of *Paleofavosites subelongus* can be quite different from one transverse section to another, both within and between coralla. For this reason, we used this species as an example in an examination of the relationship between favositid corallite size and polygonality (number of sides) (see Young and Elias, 1993). Differences in the variability of corallite dimensions between transverse sections from a single corallum are apparently related to rate and periodicity of corallite increase (Young and Elias, 1993, p. 288; see also Scrutton and Powell, 1980, p.

Table 11.—Interlocality variation in quantitatively defined morphologic characters of *Propora thebesensis* in the east-central United States. "A" and "B" refer to frequency of data points above and below arbitrary lines in Text-figure 14B, D, F.

	section-intervals			
characters	*23-2*	*31-1 and 31-1b*	*14-1*	*15-1*
tabularium area : corallite area				
A (tabularia closely spaced)	1 (7%)	8 (67%)	11 (79%)	4 (40%)
B (tabularia farther apart)	13 (93%)	4 (33%)	3 (21%)	6 (60%)
spacing of tabulae and dissepiments				
A (elements close together)	7 (100%)	1 (17%)	1 (9%)	—
B (elements farther apart)	0 (0%)	5 (83%)	10 (91%)	—
wall thickness and septal development				
A (walls thick, septa longer)	9 (69%)	1 (10%)	3 (33%)	1 (20%)
B (walls thin, septa short or absent)	4 (31%)	9 (90%)	6 (67%)	4 (80%)

480). New corallites expanded slowly due to the physical constraints caused by corallite packing (Young and Elias, 1993, pp. 289, 290, table 1). The size-frequency distribution of corallites having six and more sides on any given transverse section of *P. subelongus* is virtually normal. This supports the recognition of such corallites as mature individuals (see Young and Elias, 1993, pp. 284, 286, fig. 3).

Corallite size is correlated with the degree of development and thickening of several skeletal characters, including wall thickness, relative septal length, and the diameter of corner pores (see *Intraspecific variation,* p. 85). The relationship between average corallite dimension and pore diameter is comparable to that described by Tesakov (1973, figs. 8, 9) for *Favosites* Lamarck and *Calamopora* Goldfuss (*Paleofavosites*) from the Silurian of Siberia. However, a relationship between corallite size and the development of pores, wall thickness, and septal length has not, to our knowledge, been previously documented. Such a relationship certainly has not been observed in any of the other tabulates included in the present study. The correlation among these characters supports the idea that growth of favositid corallites was largely controlled by structural constraints imposed by colony design; these constraints apparently extended beyond the physical corallite packing discussed by Young and Elias (1993).

Variation in mean corallite size is correlated with general differences in colony growth form between localities. Coralla having domical growth forms and flat bases tend to have larger corallites than do those having bulbous or columnar forms and conical bases. This difference may be related to the primary growth habit of each corallum; an initially broad divergence of corallites provided more space for corallites to expand to large sizes within the corallum. The relationship between average corallite dimension and colony form is complex because form could change during astogeny, and factors such as colony reorientation and partial mortality could have affected the final form.

The shape of the corallum base itself seems to have resulted more from a response to local conditions than from deterministic growth, although the initial pattern indicates a degree of genetic control. Serial sections through the absolute base of a corallum show that the protocorallite (formed by the polyp that founded the colony) was joined initially by four hysterocorallites (formed by polyps that arose through budding). This pattern is very similar to that described by Girty (1895) for four species of *Favosites,* except that the location of the hysterocorallites in Girty's specimens was generally more regular than is the case for the corallum of *Paleofavosites subelongus.* Subsequent growth of the base, however, shows no indication of dominance on the part of the protocorallite or the initial hysterocorallites, and the continued growth of any corallite seems to have been related to its position in the corallum rather than to "seniority." The shapes of bases of individual coralla are consistent with local environmental conditions inferred from other indicators, such as lithology and abrasion of coralla (see *Growth Form,* p. 29).

Table 12.—Interlocality variation in qualitatively defined morphologic characters of *Paleofavosites subelongus* in the east-central United States. P = predominant, C = common, R = rare or weakly developed, A = absent.

	sections/section-intervals						
characters	*31-1*	*14-1*	*15-1*	*18*	*S of Clarks-ville*	*near Edge-wood*	*32-1z*
columnar forms	—	C	A	—	—	—	R
high bulbous forms	—	C	C	—	—	—	R
low bulbous forms	—	C	C	—	—	—	R
high domical forms	—	C	A	—	—	—	C
low domical forms	—	C	C	—	—	—	C
long septa	A	C	R	P	C	P	C
mid-wall pores	A	R	A	A	A	R	R
widely spaced tabulae	P	C	C	C	P	C	P
closely spaced tabulae	R	C	C	C	R	C	R
cyclomorphic thickening	A	C	C	R	C	R	R

Tabulations of morphologic characters (Tables 12, 13) indicate that similar morphotypes occur at several localities, and that much of the interlocality variation is not systematic. It is difficult to make general comparisons between the distribution of growth form and that of most other characters because form data for most localities are not available; correspondences between form and average corallite dimension are discussed above. Coralla from Section-interval 31-1 (Thebes North) lie at one end of the spectrum of variation in internal morphology, characteristically having small corallites, short septa, widely spaced tabulae, and little or no cyclomorphic thickening. Specimens from 5 km south of Clarksville, Missouri, also have small corallites and widely spaced tabulae, but some of these have longer septa and a higher degree of cyclomorphic thickening. Coralla from Section-interval 14-1 (Higginbotham Farm) and Section-interval 15-1 (Calumet) are highly variable, including most of the range of variation of this species, whereas those from Section-interval 18-1 (Kissenger) and from the Cyrene Formation near Edgewood, Missouri, generally have long septa, variable spacing of tabulae, and rare cyclomorphic thickening. The suite of coralla from Section-interval 32-1z (Thomson East) is distinctive; these possess large, thin-walled corallites with widely spaced tabulae.

The occurrence of mid-wall pores in this species may have stratigraphic and evolutionary significance. Mid-

Table 13.—Interlocality variation in quantitatively defined morphologic characters of *Paleofavosites subelongus* in the east-central United States. "A" and "B" refer to frequency of data points above and below arbitrary lines in Text-figures 25A, B, 26A; c.v. = coefficient of variation.

	sections/section-intervals				
characters	*31-1*	*14-1*	*15-1*	*S of Clarksville*	*32-1z*
average corallite dimension					
A (larger corallites)	0 (0%)	19 (50%)	2 (29%)	0 (0%)	24 (73%)
B (smaller corallites)	6 (100%)	19 (50%)	5 (71%)	5 (100%)	9 (27%)
c.v. of avg. corallite dimension and c.v. of polygonality					
A (more variable size and polygonality)	4 (67%)	23 (61%)	5.5 (79%)	1 (20%)	16 (48%)
B (less variable size and polygonality)	2 (33%)	15 (39%)	1.5 (21%)	4 (80%)	17 (52%)
wall thickness and average corallite dimension, 6+ sides					
A (walls relatively thick)	—	18 (58%)	3 (43%)	—	2 (33%)
B (walls relatively thin)	—	13 (42%)	4 (57%)	—	4 (67%)

wall pores are absent in coralla from all stratigraphic intervals considered to be latest Ordovician (Gamachian), such as Section-intervals 23-2 and 23-3 (Lawrence Quarry), and Section-interval 31-1. They are, however, found in small numbers in some intervals where rocks are possibly earliest Silurian (early Rhuddanian?; *e.g.,* Section-interval 14-1) or definitely earliest Silurian (early Rhuddanian; *e.g.,* Section-interval 32-1z). This pattern, along with the greater abundance of mid-wall pores in the slightly younger (late Rhuddanian), apparently descendant species *Paleofavosites* sp. cf. *P. subelongus* from Section-interval 32-1c (Thomson East), suggests that this character appeared within the species lineage.

Paleofavosites adaensis.—This species exhibits little intercorallum variation in most morphologic characters, but there are distinct differences between localities for corallite size distributions and spacing of tabulae. These characters show a correlation with colony growth form (see *Intraspecific variation,* p. 93). At those localities where forms are bulbous or domical, corallite size distributions are somewhat variable and tabulae are widely spaced. Where coralla have tabular forms, corallite size distributions are regular and tabulae are more closely spaced.

Aulopora sp. A.—This species occurs at two localities. Variation in corallite size distribution for the two specimens from Section-interval 23-2 (Lawrence Quarry) shows an unusual pattern. Visual observation of both specimens suggests that each includes several small coralla comprising one or a few corallites; corallites expanded rapidly above their bases and are rarely observed to be connected with one another (Pl. 20, fig. 1). This suggestion is also supported by the frequency distribution of corallite and tabularium sizes in one specimen, which is dominated by small corallites (see *Intraspecific variation,* p. 98). In contrast with this, the size-frequency curve for a single, larger auloporid corallum from the Devonian of southwest England (Scrutton, 1990, fig. 11a) is approximately normal, and is similar to the curves commonly seen for massive coenenchymal Tabulata.

COMPARISONS OF SPECIES

Comparisons of the patterns of variation in different species indicate that inherent variabilities of different coral orders are not the same, and that certain types of variation tend to recur among species and among orders. Some of the general similarities and differences among taxa are linked principally to the structural factors that controlled the ways in which colonial corals were able to grow. Genotypic and ecophenotypic factors acted in concert with the structural control of growth to determine variation within the individual species.

Degrees of variability.—From the discussions under *Variation in Individual Species,* above, it is apparent that some colonial coral species are much more variable than are others. The possible causes of such differences in variability must be considered, because the limits of variability must be known in order to properly define species within each order. Species belonging to some orders have more variable corallite sizes due to inherent design constraints. Differences in variability are also significant because they may reflect disparity in the morphologic plasticity of species, which may explain why some species were able to live in a greater variety of environments than were others.

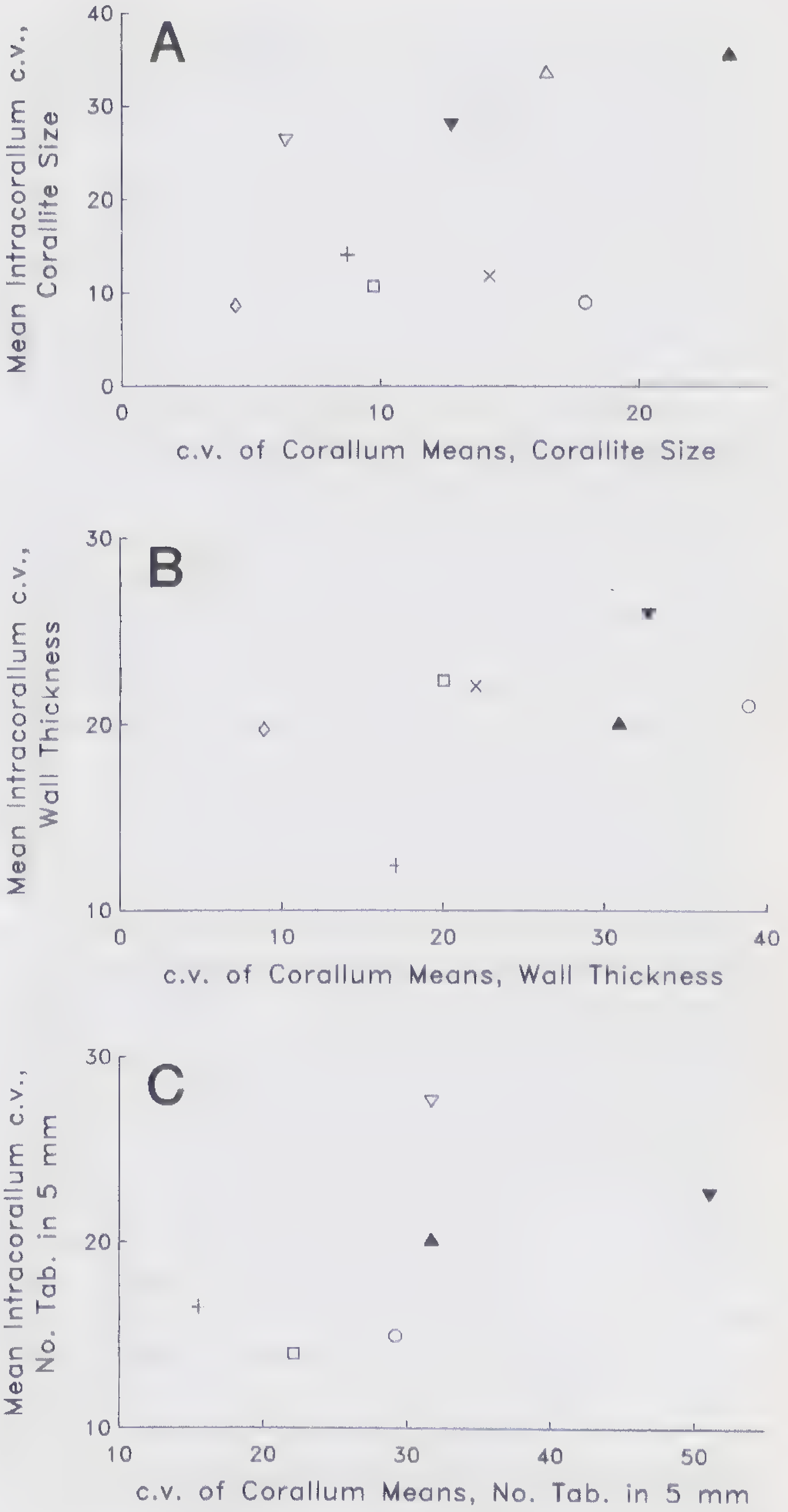
Differences in variability of fossil invertebrate taxa are quite commonly discussed in the literature, but numerical comparisons of the amount of variation are relatively rare. For a numerical description of intracorallum and intercorallum variability for each parameter, we follow Oliver (1968, pp. 27, 28), Scrutton (1989, pp. 39, 40), and Stearn (1989, pp. 45, 46) in using the coefficient of variation (c.v.) (Simpson *et al.,* 1960). The c.v. can be readily used to compare different types of numerical data because it is dimensionless. It is generated using the following formula:

$$\text{c.v.} = \frac{\text{standard deviation}}{\text{mean}} \times 100.$$

Graphs of mean intracorallum c.v. *versus* the c.v. of corallum means are plotted for three parameters: corallite size, wall thickness, and spacing of tabulae (Text-fig. 11). Intracorallum variability of corallite size for each species of *Paleofavosites* (Order Favositida) is two to three times as great as for any species of *Propora* (Order Heliolitida), or *Halysites* and *Catenipora* Lamarck (Order Halysitida) (Text-fig. 11A). A similar pattern was noted by Scrutton (1989, p. 40, fig. 4b) in a comparison of favositids and heliolitids. The basis for high intracorallum variability in corallite size of favositids is in their design. Lateral expansion of favositid offsets was slow, with rates governed by the lateral expansion of the growth surface and the degree of contraction of surrounding corallites; for this reason transverse sections frequently include substantial numbers of immature individuals (see Young and Elias, 1993, pp. 283, 288, fig. 2). The coenosteal and cateniform growth habits of heliolitids and halysitids permitted new corallites to expand much more rapidly. Most of the species of *Paleofavosites* included in the present study have intraspecific variabilities for mean corallum corallite size similar to those of the other tabulates. The one exception is *Paleofavosites subelongus;* the greater intraspecific variability of size in that species may be related to its ability to grow in a broad variety of environments (see *Paleoenvironments,* pp. 33, 34).

Although intracorallum and intraspecific variation in wall thickness can be substantial (Text-fig. 11B), there are no obvious differences among orders. Variation in wall thickness is not related in any recognizable way to the structural design of most of these taxa; the lack of such a connection probably accounts for the absence of distinctions for this character.

The graph for spacing of tabulae indicates that both intracorallum and intraspecific variability are greater for species of *Paleofavosites* than for other taxa (Text-fig. 11C). This greater variability appears to be related to two factors: cyclomorphic growth and interlocality variation. In general, the species of *Paleofavosites* occurring in the study region show a greater amount of cyclomorphic variation in spacing of tabulae than do the other colonial corals. Cyclomorphic growth patterns are particularly marked in *Paleofavosites* sp. A (Pl. 19, fig. 12), explaining the large mean intracoral-



Text-figure 11.—Comparison of coefficients of variation (c.v.) for selected parameters in several species of Tabulata from the east-central United States. **A**, Mean intracorallum c.v. *versus* intraspecific c.v. of corallum means for corallite size (tabularium diameter of heliolitids, tabularium dimension (length) of halysitids, average corallite dimension of favositids). **B**, Mean intracorallum c.v. *versus* intraspecific c.v. of corallum means for wall thickness. **C**, Mean intracorallum c.v. *versus* intraspecific c.v. of corallum means for number of tabulae in unit 5 mm. Graphs are based on data included in Tables 15, 18, 19; species included in graphs all had four or more coralla measured for the given parameter. Symbols for species: □ *Propora thebesensis*; ○ *Propora savagei*; ◇ *Propora speciosa*; + *Halysites alexandricus*; × *Catenipora lawrencica*; ▲ *Paleofavosites subelongus*; △ *Paleofavosites* sp. cf. *P. subelongus*; ▼ *Paleofavosites adaensis*; ▽ *Paleofavosites* sp. A.

lum c.v. for that species. In *Paleofavosites adaensis,* different tabular spacings are associated with the variation in corallum growth form seen at different localities; this is responsible for the great variability of corallum means for the species.

Among the non-favositid corals, *Propora savagei* and *Propora speciosa* are remarkable for representing the extremes of intraspecific variability in corallite size and wall thickness. The remarkable consistency among specimens of *P. speciosa* has already been commented upon (see *Propora speciosa,* p. 38). The high degree of intraspecific variability in *P. savagei* reflects the differences between coralla from Section 20 (Short Farm) and those from other localities (see *Discussion,* p. 58).

Shared patterns of variability.—Species of massive Tabulata having coenenchymal and cerioid growth habits both show connections between external corallum growth form and aspects of internal morphology that are related to corallite size and packing. In *Propora thebesensis,* coralla having densely spaced tabularia tend to exhibit a greater variability of tabularium diameter than do those having more broadly spaced tabularia. Tabularia are often more densely spaced at localities where taller growth forms predominate, and more broadly spaced where lower growth forms are common. The pattern for *Paleofavosites adaensis* is analogous; corallite size distributions are more variable at localities where forms are bulbous or domical than at localities where tabular forms predominate. The situation for *Paleofavosites subelongus* is slightly different; the internal parameter related to growth form is average corallite dimension (corallite size). Coralla of *P. subelongus* having domical growth forms and flat bases tend to have larger corallites than do those having bulbous or columnar forms and conical bases.

In each of these cases, control on tabularium and corallite size was probably exerted by the internal space constraints determined by external corallum form. Where external forms restricted lateral expansion of the individual modules, tabularia or corallites became smaller and/or expanded more slowly (producing more variable size distributions). The influence of environmental factors on corallum growth form was apparently similar in *Propora thebesensis* and *Paleofavosites subelongus* (see p. 28), and variation in internal characters of these species may have been partly under environmental control.

SYSTEMATIC PALEONTOLOGY

INTRODUCTION

Analysis of variation is integral to the species concept for Paleozoic colonial corals. The general approach that we use is similar to that outlined by Scrutton (1989, pp. 40, 41). Valid species can be recognized only when intraspecific variation based on a number of coralla is thoroughly documented. A very high degree of intraspecific variability can be accepted, but variation in important numerical and non-numerical characters must be reasonably continuous. Species are separated from one another by morphologic gaps (*e.g.,* see Young and Noble, 1990b, fig. 2). In this study we include separate descriptions of intraspecific variation under those species for which sufficient data are available; an overview and synthesis that compares variation in the different species and orders is presented above (see *Aspects of Intraspecific Variation,* pp. 34–42). All aspects of morphology that can be described, including astogeny, corallite increase, microstructure, and growth form, are considered when defining species. In general, the most useful characters for species discrimination are the form of basic structural elements such as walls, septa, and tabulae, and certain measured parameters including tabularium or corallite diameter and corallite area (see *Biometric Methods,* pp. 43, 44).

In many respects, the systematic difficulties involved in the discrimination of Paleozoic colonial coral species are comparable to the problems faced by workers examining living corals of the subclass Scleractinia Bourne (*e.g.,* Coates, 1984). Some species of modern corals show little variability, but others are extremely variable (Best *et al.,* 1984). Analysis of large numbers of scleractinian colonies is essential for determining patterns of intracolony and intraspecies variability (*e.g.,* see Veron and Pichon, 1976; Foster, 1985).

Our suprageneric classification is similar to that given in Hill (1981), with two significant exceptions. First, we consider the Halysitida to be a separate order, rather than a suborder of the Heliolitida. Second, the subfamily Paleofavositinae Sokolov is included as a junior synonym of the Favositinae Dana. Explanations of these differences in approach are provided in the discussions under those groups, below. Suprageneric taxa and genera are discussed if our work has increased the knowledge and understanding of the group.

Many of the morphologic terms that we use to describe both tabulate and rugose corals follow Hill (1981, pp. F6–F36, F430–F456). Some terms for heliolitid morphology are taken from Dixon (1974). Categories for corallum growth form are described in *Growth Form* (pp. 27, 28). General terms for corallite increase are from Oliver (1968, pp. 19–21) and (Hill, 1981, pp. F437, F438); descriptors of increase in halysitids are after Webby and Semeniuk (1969, pp. 353–356) and Webby (1975). Detailed terms are not used to distinguish astogenetic stages because this would impose an arbitrary structure on phenomena that are poorly understood.

A total of 361 specimens from the east-central United States are identified herein; these are assigned to 21 species. Both transverse and longitudinal thin sections were made of all collected coralla; specimens were identified and measured if possible. Species descriptions and diagnoses are based on all identified material. A group of thoroughly documented, conspecific coralla is assigned to a previously described species if a definite identification can be made, using comparison with type material. A new species is named if sufficient material is available so that we can accurately assess morphology and variability, and can not assign that material to a previously described species. In some cases, a group of coralla clearly belongs to a single species, but can not be completely described due to insufficient numbers or poor preservation. If it has obvious affinities with or is comparable to a known species, it is named with "sp. aff." or "sp. cf.," respectively. Such a group of conspecific coralla is assigned a letter designation ("sp. A") if it is not sufficiently similar to a known species. The designation "sp." is used for a group of coralla belonging to *Palaeophyllum* because we are not certain that all included coralla are conspecific.

Each synonymy includes those taxa we consider to be synonymous, along with possible synonyms and others that are very similar. A similar taxon that is not definitely synonymous with the described group is given the appropriate designation, as follows: [*aff.*] if it has definite affinities, [*cf.*] if it is comparable, and [?] if it is a questionable synonym.

BIOMETRIC METHODS

Many Paleozoic colonial corals are morphologically simple, possessing several characters that are easily quantified. Such characters are good indicators of variation, but they should be assessed carefully, and must not be used to the exclusion of qualitatively defined features for species discrimination. Many of the measurements applied here are the same as or similar to parameters used in the following studies: Dixon (1974, pp. 568–570) and Young and Noble (1990a, pp. 44, 45) for Heliolitida; Young *et al.* (1991, pp. 715, 716) for Halysitida; and Sutton (1966, p. 257) and Young and Elias (1993) for Favositida. Measurements are made on the mature part of each corallum, if it can be recognized. For linear measurements, a sample of 20 corallites per corallum is considered to give a reasonable representation of that specimen (Oliver, 1968, p. 27; Dixon, 1974, p. 568; Scrutton, 1989, p. 40). Where possible, at least 20 corallites are measured within a contiguous area on each thin section for each appropriate parameter. An exception is made for average corallite dimension and polygonality of favositids, where all corallites in a contiguous area are measured until data are obtained on at least 20 corallites having six and more sides (such corallites are considered to be adults; see Young and Elias, 1993). Biometric methods pertaining to growth form are described in *Growth Form* (pp. 27, 28).

The following parameters are measured or counted on transverse sections:

Tabularium diameter (TaD).—For heliolitids, the order Auloporida Sokolov, and tetradiids, this character is measured internally from wall to wall where walls are least thickened by septal development.

Tabularium dimensions (TaD (L), TaD (W)).—Length (L, along the rank) and width (W, across the rank) of halysitid tabularia are measured separately because most halysitid corallites are ovate or elliptical in transverse section. Measurement is done internally from wall to wall.

Tabularium area (TaA).—For heliolitids, tabularium area is calculated from the diameter. For halysitids, it is calculated as the area of an ellipse based on the tabularium dimensions (length and width).

Average corallite dimension (ACD (all), ACD (6+)).—This parameter, measured in favositids, is similar to the average transverse axis measurement of Sutton (1966, p. 257). Two measurements of dimension for each corallite are made at right angles to one another, between corallite midwalls. The mean of these is used to describe corallite size. For a corallite that is not equidimensional, the axis around which the corallite is closest to being bilaterally symmetrical is used to orient the first measured dimension. Data are presented separately for all measured corallites and for those having six and more sides.

Corallite diameter (CoD).—The external corallite diameter is measured for auloporids, tetradiids, and rugosans.

Corallite area (CoA).—This parameter is quantified for heliolitids and favositids. A unit area of 1 cm^2 is placed on the part of the transverse section on which measurements of tabularium diameter or average corallite dimension are made; all corallites within that area are counted. Half and quarter corallites are included in the count. The mean corallite area, in mm^2, is calculated from the inverse of this count.

Tabularium area : corallite area (TaA:CoA).—The ratio between tabularium area and corallite area of heliolitids is quantified as a measure of density of tabularium spacing.

Polygonality (Pol).—For favositids, polygonality (the number of sides per corallite) is determined as the number of other corallites a particular corallite is in contact with.

Tubule diameter (TuD).—For heliolitids having tubular coenenchymes, internal diameter of each tubule is measured.

Tubule dimensions (TuD (L), TuD (W)).—For halysitids having tubules between their corallites, internal tubule dimensions are separated into length (L, along the rank) and width (W, across the rank).

Wall thickness (WT).—This character is measured for all corals. In heliolitids, thickness of the tabularium wall is measured between septa, where it is least affected by trabecular thickening. In halysitids, wall thickness is measured at the midpoint of the side of each corallite. In favositids, the thickness of each shared corallite wall is measured between septa, where it is less affected by thickening. In auloporids and tetradiids, the corallite wall is measured between septa, where it is least affected by thickening. For rugosans, this character is measured at the midpoint between a pair of septa.

Pore diameter (PoD).—The diameter of corner pores is measured in favositids.

Length of septa (LS).—For heliolitids, halysitids, and auloporids, the length of septa in each corallite is determined as a percentage of the tabularium radius. In favositids and tetradiids, the percentage of the corallite radius is used. For rugosans, the length of major septa is determined as a percentage of the corallite radius.

Number of major septa (NS).—The number of major septa in each rugosan corallite is counted.

The following parameters are measured or counted on longitudinal sections:

Number of tabulae in 5 mm (Ta5).—For all groups, the number of corallite tabulae in 5 mm is counted along the axis of each corallite. One end of the unit 5 mm is placed directly over one tabula, which is not included in the count.

Number of septa in 5 mm (Se5).—For favositids, the number of septal spines in 5 mm is counted along the wall of each corallite. One end of the unit 5 mm is placed directly over one septum, which is not included in the count.

Number of dissepiments in 5 mm (Di5).—The number of heliolitid coenenchymal dissepiments in 5 mm is measured along a vertical transect at the midpoint between two tabularia. One end of the unit 5 mm is placed directly over one dissepiment, which is not included in the count.

Number of tabulae in 5 mm : number of dissepiments in 5 mm (Ta5:Di5).—The ratio between vertical densities of tabulae and dissepiments in heliolitids is calculated as a measure of the relative spacing of these horizontal elements.

Thickness of cycles (TC).—The thickness of cycles is measured in coralla exhibiting obvious cyclomorphic variation in density of spacing and thickening of skeletal elements. A cycle is defined as one pair of dense and less dense growth bands.

COLLECTORS AND REPOSITORIES

Specimens examined during this study are identified by a repository abbreviation and catalogue number. Unless stated otherwise, they were collected by R. J. Elias, G. A. Young, and V. L. F. Young in 1990. Abbreviations of repositories are listed below.

GSC:	Geological Survey of Canada, Ottawa, Ontario, Canada.
ROM:	Royal Ontario Museum, Toronto, Ontario, Canada.
UI:	University of Illinois at Urbana–Champaign, Urbana, Illinois, U.S.A.
USNM:	National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.
YPM:	Peabody Museum of Natural History, Yale University, New Haven, Connecticut, U.S.A.

SYSTEMATICS

Class **ANTHOZOA** Ehrenberg, 1834

Subclass **TABULATA**
Milne-Edwards and Haime, 1850

Order **HELIOLITIDA** Frech, 1897

Diagnosis.—Tabulata having massive coralla of variable growth form. Tabularia separated by coenenchyme. Septa number 12, each consisting of a trabecular or laminar base that may possess a row of distinct spines; may be absent. Tabulae commonly complete. Increase coenenchymal.

Remarks.—Our concept of the Heliolitida is essentially the same as that outlined by Hill (1981, p. F602) for the Heliolitina Frech. Hill (1981, pp. F602, F603) included the Halysitina Sokolov in the Heliolitida. We consider the Halysitida to be a separate order (see *Discussion* under Order Halysitida, pp. 66, 67).

Family **PROPORIDAE** Sokolov, 1949

Genus **PROPORA**
Milne-Edwards and Haime, 1849

Propora Milne-Edwards and Haime, 1849, p. 262.
Lyellia Milne-Edwards and Haime, 1851, pp. 150, 226.
Pinacopora Nicholson and Etheridge, 1878, p. 52.
Calvinia Savage, 1913, pp. 65, 66 [*non* Nutting, 1900].
Cavella Stechow, 1922, p. 152.
Koreanopora Ozaki, 1934, p. 68.
[?] *Acdalopora* Bondarenko, 1958, p. 215.
[?] *Mcleodea* Flower and Duncan, 1975, pp. 186, 187.

Type species.—By monotypy: *Porites tubulata* Lonsdale (1839, p. 687, pl. 16, figs. 3, 3a–f); Woolhope

Limestone (upper Lower Silurian, Wenlock), Welsh Borderland, U.K.

Diagnosis.—Proporidae with tabularia of smooth or crenulate outline, separated from one another by coenenchyme composed of dissepimentate plates. Twelve septa have basal ridges that may bear spinose adaxial extensions; septal bases commonly exhibit trabecular thickening which may extend outward into coenenchyme. Other trabeculae may occur between septa in corallite walls, or in coenenchyme. Corallite walls composed of vertically oriented trabeculae, or with lamellar appearance where trabeculae are not developed; complete or incomplete. Tabulae usually complete.

Discussion.—Our concept of *Propora* is similar to those recently outlined by Dixon (1974, p. 570), Laub (1979, pp. 331, 332), Hill (1981, p. F612), Scrutton (1985, p. 35), and Young and Noble (1990b, pp. 187, 188). The present examination of species from the east-central United States, however, demonstrates that members of this genus can have a wide variety of wall structures.

Calvinia (= *Cavella*) is synonymized with *Propora*, following re-examination of the type material. Savage's (1913) recognition of *Calvinia* as a distinct genus was based on the incorrect interpretation of vertically oriented coenenchymal trabeculae as tubules. The type specimen of *Calvinia edgewoodensis* (UI X-850), from the Leemon Formation (uppermost Ordovician, Gamachian) at the Gale Section is conspecific with *Propora speciosa* (see *Discussion* under *Propora speciosa*, pp. 60, 61).

The other genera included in the synonymy have been discussed in one or more recent studies, but a few points require further discussion. *Mcleodea*, from the Aleman Formation of Texas (Upper Ordovician, Maysvillian–Richmondian; Sweet, 1979, fig. 4), is very similar to *Propora*. It has a coenenchyme that is almost tubular where tabularia are closely spaced, however, and has walls that are composed of the lateral edges of coenenchymal dissepiments in some places. Young and Noble (1990b, p. 188) noted that some specimens of *Propora exigua* (Billings) from the Lower Silurian of northern New Brunswick have coenenchymes of similar character. Corallite walls composed of the lateral edges of coenenchymal dissepiments occur in *Propora* sp. A from the Sexton Creek Limestone of southern Illinois (lower Lower Silurian, Lower? Llandovery) (Pl. 8, fig. 2) and in *Propora americana* (Milne-Edwards and Haime) from the Lower Silurian of northern New Brunswick (Young and Noble, 1990b, fig. 6.4). For these reasons, we tentatively synonymize *Mcleodea* with *Propora*.

Young and Noble (1990b, pp. 187, 188) considered *Rotalites* Leleshus (1974, p. 97), from the Upper Silurian of Tadzhikistan, to be a junior synonym of *Propora*. The dissepiment-like longitudinal folds that occur in the walls of *Rotalites* are, however, very distinctive. We recognize it as a separate genus, almost certainly derived from *Propora*.

Propora thebesensis (Foerste, 1909)

Plate 1, figures 1–11; Plate 2, figures 1–12;
Plate 3, figures 1–11; Plate 4, figures 1–10

Heliolites affinis Billings, 1865, pp. 427, 428 [*partim*]; 1866, pp. 5, 6 [*partim*].

Lyellia affinis (Billings, 1865). Lambe, 1899, pp. 84, 85 [*partim; non* pl. 5, figs. 1, 1a]; Twenhofel, 1928, p. 133 [*partim*].

[?] *Propora conferta* Milne-Edwards and Haime, 1851. Lindström, 1899, pp. 93, 94 [*partim*], pl. 9, figs. 11, 12 [*non* pl. 8, figs. 32–39, pl. 9, figs. 1–10, 13–23]; Bolton, 1980, p. 20, pl. 2.4, figs. 1–3, 9, 10, pl. 2.5, fig. 7.

Lyellia thebesensis Foerste, 1909, p. 95, pl. 4, figs. 69a, 69b; Savage, 1913, pp. 66, 67, pl. 3, figs. 6, 7; 1917, pp. 116, 117, pl. 5, figs. 6, 7.

[*cf.*] *Propora* cfr. *magnifica* Počta, 1902. Ozaki, 1934, p. 67, pl. 10, figs. 9, 10, pl. 11, fig. 1.

[*cf.*] *Propora yabei* Ozaki, 1934, pp. 67, 68, pl. 11, figs. 2, 3.

[*cf.*] *Propora conferta* var. *tunicata* Sokolov, 1950b, p. 229, pl. 7, figs. 1, 2.

[*cf.*] *Propora cancellatiformis* Sokolov, 1950b, pp. 230, 231, pl. 7, figs. 3, 4, pl. 8, figs. 1, 2.

[?] *Lyellia thebesensis paucivesiculosa* Bolton, 1957, pp. 64, 65, pl. 6, figs. 1–7.

Propora conferta Milne-Edwards and Haime, 1851. Dixon, 1974, pp. 570–580, figs. 5, 6, pl. 1, figs. 1–9, pl. 2, figs. 1–9; Bolton, 1981a, pl. 1, figs. 6, 7, pl. 2, figs. 6, 7, pl. 3, figs. 1, 2, pl. 8, figs. 13, 14 [*non* pl. 9, fig. 1, pl. 11, figs. 1, 2].

Propora thebesensis (Foerste, 1909). Elias and Young, 1992, figs. 3c, 3d; Young and Elias, 1993, pl. 1, figs. 5–10.

Diagnosis.—*Propora* with smooth-walled or crenulate tabularia, adult tabularium diameters usually 0.9–1.4 mm; tabularium area about 30–70% of corallite area. Where present, septa are composed of thickened ridges; discrete spines absent. Coenenchymal dissepiments globose; coenenchyme lacks vertical rods and plates.

Description of coralla.—Coralla are of low and high bulbous and domical, and low columnar growth forms (Table 14; Pl. 2, fig. 11, Pl. 3, figs. 4, 8). Sizes of coralla range from 10–147 mm wide and 11–73 mm high; most are small.

In transverse section, tabularia are smooth-walled and subcircular (Pl. 2, fig. 8), slightly crenulate (Pl. 1, fig. 6, Pl. 3, figs. 1, 5, Pl. 4, fig. 4), or with marked trabecular thickenings that rarely develop exothecal extensions (Pl. 1, figs. 1, 5, 7, Pl. 2, figs. 5, 6). Adult tabularia commonly have diameters of 0.9–1.4 mm (Table 15). Tabularia are close-spaced to very close-spaced; tabularium area is usually 45–65% of corallite area (Table 15). Where tabularia are closely spaced, tabularium shape may become subpolygonal (Pl. 2, fig.

Table 14.—Growth forms of coralla by species and collection intervals in the east-central United States.

	growth forms						
species *section-intervals (n = no. of coralla)*	*bulbo-columnar*	*domico-columnar*	*high bulbous*	*high domical*	*low bulbous*	*low domical*	*tabular*
Propora thebesensis							
23-2 (n = 6)	—	—	—	3	1	2	—
31-1 and 31-1b (n = 10)	7	—	1	—	—	2	—
14-1 (n = 10)	2	1	3	2	2	—	—
15-1 (n = 4)	—	—	3	1	—	—	—
16-2 (n = 1)	—	—	1	—	—	—	—
other (n = 3)	1	—	—	1	—	1	—
all (n = 34)	10	1	8	7	3	5	0
Propora savagei							
20-1 (n = 1)	1	—	—	—	—	—	—
31-1 and 31-1b (n = 2)	—	—	2	—	—	—	—
all (n = 3)	1	0	2	0	0	0	0
Halysites alexandricus							
23-2 (n = 1)	—	—	1	—	—	—	—
31-1 and 31-1b (n = 2)	—	—	—	—	1	1	—
37-1 (n = 1)	—	—	—	—	—	1	—
all (n = 4)	0	0	1	0	1	2	0
Paleofavosites subelongus							
31-1 and 31-1b (n = 1)	—	—	—	—	—	1	—
14-1 (n = 24)	2	—	7	6	3	6	—
15-1 (n = 4)	—	—	2	—	1	1	—
16-1 (n = 1)	—	—	—	1	—	—	—
18-1 and 18-2 (n = 2)	—	1	1	—	—	—	—
32-1z (n = 23)	—	1	2	11	1	8	—
all (n = 55)	2	2	12	18	5	16	0
Paleofavosites sp. cf. *P. subelongus*							
32-1c (n = 2)	—	—	1	—	—	1	—
Paleofavosites adaensis							
35-1 (n = 2)	—	—	—	—	—	—	2
Paleofavosites sp. A							
5-2 and 6-1 (n = 3)	—	—	—	—	—	2	1

1, Pl. 3, figs. 6, 9, Pl. 4, fig. 6); in extreme cases the character of growth mimics that of *Favosites.* In longitudinal section, tabularia are straight in the axial part of the corallum but are often strongly curved in more marginal parts (Pl. 2, fig. 9, Pl. 3, fig. 4). In coralla with close spacing of tabularia, adjacent individuals may have walls in contact for a substantial portion of their length (Pl. 3, fig. 10, Pl. 4, fig. 7).

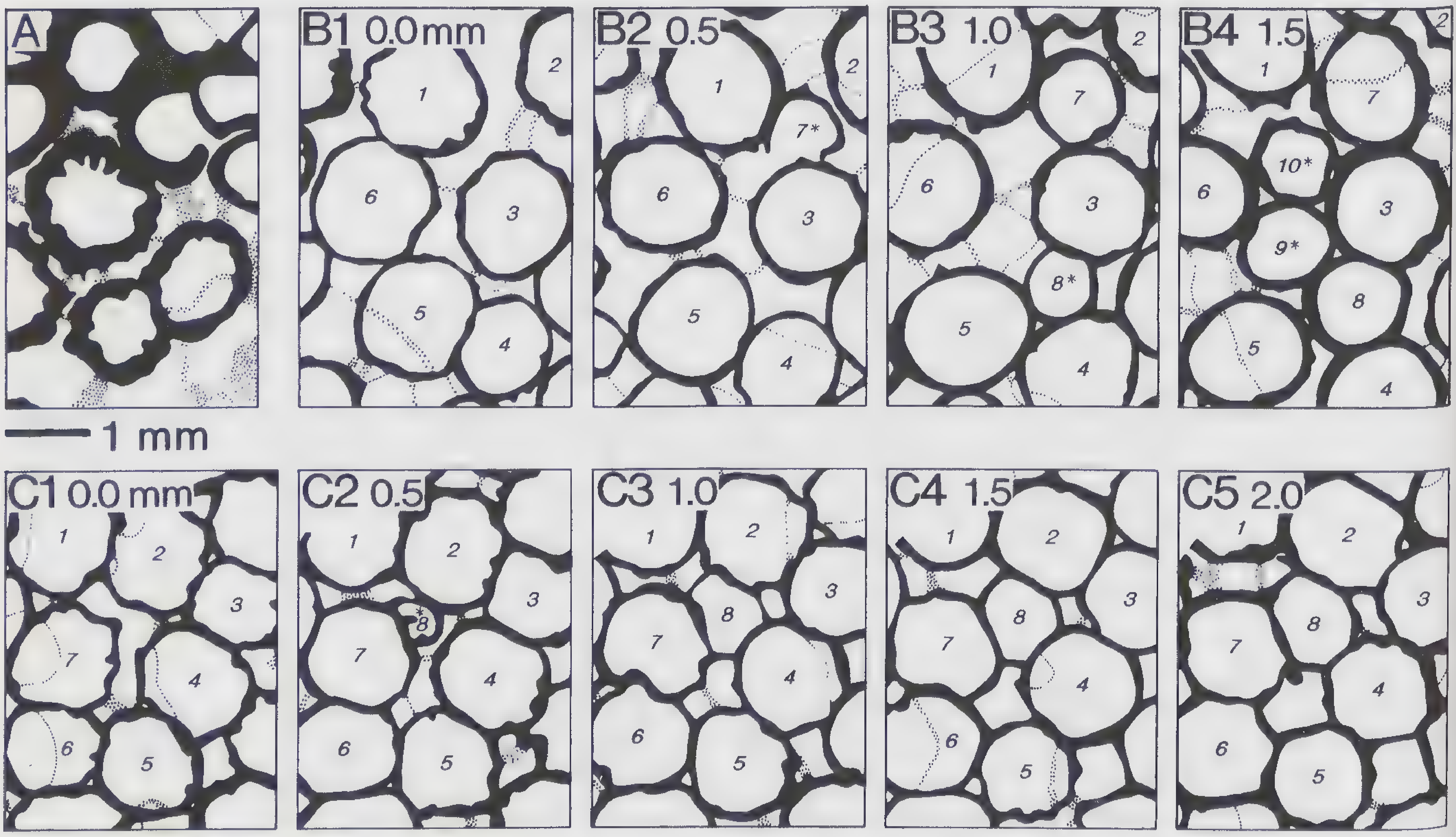
Walls are thin and smooth, or have slight to pronounced trabecular thickening at septa. Wall thickness is commonly 0.06–0.10 mm (Table 15). Septa are variably developed, absent to 12 pronounced thickened ridges; trabecular thickening varies cyclomorphically (Pl. 1, figs. 5, 10). In transverse section, septal thickening may be variably developed within a single corallite (Pl. 2, fig. 6). Septal length is commonly 0–25% of tabularium radius (Table 15). Discrete septal spines are absent; small ragged extensions are very rarely present at inner edges of trabeculae.

Tabulae are of moderate thickness; flat, wavy, or slightly convex or concave (Pl. 2, figs. 4, 9); rarely strongly concave or V-shaped (Pl. 1, fig. 2). Tabulae are usually complete (Pl. 4, fig. 7), rarely incomplete (Pl. 4, fig. 8). Tabulae are widely spaced (Pl. 2, fig. 9, Pl. 3, fig. 10), averaging about eight in 5 mm (Table 15); rarely closely spaced (Pl. 1, fig. 11). Spacing and thickening of tabulae show only slight cyclomorphic variation, even where thickening of septal trabeculae is extremely variable.

In longitudinal section, coenenchyme is composed of moderately widely spaced, globose dissepiments, averaging about 15 in 5 mm; about twice as many dissepiments as corallite tabulae per unit of vertical distance (Table 15). Dissepiments are thin, but are slightly thickened near corallite walls; they may show slight cyclomorphic thickening (Pl. 1, fig. 2). Dissepiments are usually regularly arranged, but may be irregular in some parts of a corallum. Where tabularia are very

Table 15.—Biometric data for proporids from the east-central United States. *TaD* = tabularium diameter, *TaA* = tabularium area, *CoA* = corallite area, *WT* = wall thickness, *LS* = length of septa, *Ta5* = number of tabulae in 5 mm, *Di5* = number of coenenchymal dissepiments in 5 mm, *TC* = thickness of cycles; s.d. = standard deviation, c.v. = coefficient of variation.

species	*parameters*									
data	*TaD*	*TaA*	*CoA*	*TaA:CoA*	*WT*	*LS*	*Ta5*	*Di5*	*Ta5:Di5*	*TC*
Propora thebesensis										
mean	1.13 mm	1.01 mm^2	1.88 mm^2	0.54	0.080 mm	7%	7.7	14.7	0.51	—
range of colony means	0.88–1.46 mm	0.61–1.67 mm^2	1.25–2.63 mm^2	0.35–0.71	0.057–0.133 mm	0–28%	4.4–13.3	10.6–20.5	0.32–0.84	—
s.d. of colony means	0.11 mm	0.21 mm^2	0.31 mm^2	0.09	0.016 mm	8%	1.7	2.6	0.11	—
c.v. of colony means	9.7	20.8	16.5	16.7	20.0	114.3	22.1	17.7	21.6	—
minimum	0.18 mm	—	—	—	0.050 mm	—	3	8	—	—
maximum	1.65 mm	—	—	—	0.350 mm	—	18	30	—	—
mean intracolony c.v.	10.7	—	—	—	22.3	—	14.0	14.8	—	—
no. of coralla studied	84	84	67	67	48	62	72	37	37	—
Propora savagei										
mean	1.62 mm	2.11 mm^2	4.63 mm^2	0.42	0.167 mm	27%	7.2	13.1	0.56	—
range of colony means	0.98–2.06 mm	0.75–3.33 mm^2	1.75–6.90 mm^2	0.30–0.54	0.085–0.258 mm	16–44%	5.4–11.4	9.6–19.3	0.47–0.69	—
s.d. of colony means	0.29 mm	0.71 mm^2	1.52 mm^2	0.08	0.065 mm	9%	2.1	3.9	0.10	—
c.v. of colony means	17.9	33.6	32.8	19.0	38.9	33.3	29.2	29.8	17.9	—
minimum	0.45 mm	—	—	—	0.050 mm	—	3	8	—	—
maximum	2.10 mm	—	—	—	0.300 mm	—	14	23	—	—
mean intracolony c.v.	9.0	—	—	—	21.0	—	15.0	13.2	—	—
no. of coralla studied	15	15	11	11	5	8	10	5	5	—
Propora speciosa										
mean	2.49 mm	4.87 mm^2	15.52 mm^2	0.31	0.213 mm	64%	5.4	8.8	0.59	—
range of colony means	2.34–2.60 mm	4.30–5.34 mm^2	13.30–16.78 mm^2	0.27–0.37	0.181–0.225 mm	56–75%	4.8–5.8	7.8–10.3	0.54–0.64	—
s.d. of colony means	0.11 mm	0.44 mm^2	1.53 mm^2	0.04	0.019 mm	10%	0.5	1.1	0.05	—
c.v. of colony means	4.4	9.0	9.9	12.9	8.9	15.6	9.3	12.5	8.5	—
minimum	1.75 mm	—	—	—	0.125 mm	—	4	7	—	—
maximum	2.90 mm	—	—	—	0.300 mm	—	7	13	—	—
mean intracolony c.v.	8.6	—	—	—	19.7	—	15.6	11.7	—	—
no. of coralla studied	5	5	4	4	5	3	3	4	3	—
Propora sp. aff. *P. affinis*										
mean	1.17 mm	1.08 mm^2	2.84 mm^2	0.38	0.064 mm	12%	10.5	13.5	0.78	4.0 mm
minimum	0.85 mm	—	—	—	0.025 mm	—	8	11	—	2.1 mm
maximum	1.30 mm	—	—	—	0.100 mm	—	15	18	—	5.3 mm
intracolony c.v.	6.8	—	—	—	11.2	—	17.0	13.7	—	—
no. of coralla studied	1	1	1	1	1	1	1	1	1	1
Propora sp. A										
mean	2.56 mm	5.17 mm^2	25.84 mm^2	0.20	0.140 mm	78%	13.2	10.6	1.25	—
minimum	1.85 mm	—	—	—	0.125 mm	—	10	8	—	—
maximum	3.10 mm	—	—	—	0.175 mm	—	13	14	—	—
intracolony c.v.	13.0	—	—	—	5.3	—	15.2	17.9	—	—
no. of coralla studied	1	1	1	1	1	1	1	1	1	—



Text-figure 12.—Transverse sections illustrating astogeny and corallite increase in *Propora thebesensis*. **A**, Earliest growth stage of a corallum, showing group of similar thick-walled corallites; USNM 485701, Section-interval 23-2 (Lawrence Quarry). **B1**–**B4**, Serial sections showing corallite increase in axial part of a corallum having broad tabularium spacing; USNM 459087, Section-interval 23-2 (Lawrence Quarry). **C1**–**C5**, Serial sections showing corallite increase in axial part of a corallum having close tabularium spacing; USNM 459076, Section-interval 16-2 (Clinton Spring) (see also Pl. 3, figs. 8–11). Corallite walls and septa are solid, tabulae and dissepiments are stippled; scale bar is shown. For B and C, heights in mm are above an arbitrary datum within the mature part of each corallum; numbers in italics represent individual corallites; an asterisk indicates the first appearance of a particular corallite.

closely spaced, dissepiments appear as flat, horizontal plates (Pl. 3, fig. 7, Pl. 4, figs. 2, 5, 7); where tabularia are widely spaced, dissepiments become more broadly domed (Pl. 1, fig. 2, Pl. 2, fig. 4). In some places the outer edges of thickened septal trabeculae appear as small nodes or vertical plates on the upper surfaces of dissepiments (Pl. 1, fig. 2). In transverse section, dissepiments are thin and sparsely distributed (Pl. 1, figs. 1, 5). Where cyclomorphic variation in thickness of elements is pronounced, extreme thickening of septal structures may replace the coenenchyme with a dense trabecular mass between adjacent tabularia (Pl. 1, fig. 11).

Astogeny and corallite increase.—Descriptions are based principally on two serial-sectioned coralla (USNM 459076, 459087) and six serial-sliced coralla (USNM 459075, 485701, 485711, 485712, 485741, 485753). Other specimens are used for comparison.

The earliest growth stages are recognized in three coralla. In each of these, the protocorallite cannot be distinguished. Rather, a small group of up to 10 similar, closely spaced corallites occurs at the absolute base of the corallum (Text-fig. 12A); these corallites are subvertical to divergent, arising from a plate-like holotheca. In two of the three coralla, the holothecae are based on tabular stromatoporoids. The character of the initial corallites varies between coralla; they can be thin-walled or thick-walled, and have pronounced septal trabeculae (Text-fig. 12A) or are smooth-walled and almost aseptate.

Spacing of tabularia is commonly less dense above the basal part of a corallum, but in some specimens it remains very dense. Wall thickness within a corallite commonly changed during growth; if initial stages are thin-walled and aseptate, septal trabeculae may appear at 1.5–2.0 mm above the corallite's base. Cyclomorphic variation in thickening and spacing of elements is generally slight (see *Description of coralla*, above). In many coralla, some corallites extend from the base to the upper growth surface. Skeletal elements may be thick and densely spaced at the upper surface of a corallum, or they may be identical to those occurring below.

Corallite increase is coenenchymal; there are two modes of initiation depending on density of tabularium spacing. Where spacing is broad, large tabularia that are of nearly adult size were initiated on the upper surfaces of coenenchymal dissepiments, with corallite walls based directly on the dissepiments (Pl. 1, fig. 2, Pl. 2, fig. 4). In transverse section, new tabularia initiated in such settings are smooth-walled and subcircular (Text-fig. 12B1–B4; Pl. 1, fig. 3), or may possess large, thick septa before the corallite wall is complete (Pl. 1, fig. 4). New tabularia in broadly spaced settings expanded rapidly (Text-fig. 12B2–B4).

Where spacing of tabularia is close, small new tabularia were initiated against the outer walls of older individuals only where space permitted (Text-fig. 12C1–C5). At the base of each initiate there is a gradual transition in character of horizontal elements, from coenenchymal dissepiments to tabulae (Pl. 3, figs. 7, 10, 11, Pl. 4, fig. 7). In transverse section, new tabularia in close-spaced settings are smooth-walled or crenulate and are subpolygonal, with their sides compressed by the walls of adjacent individuals. Initiates in such settings expanded slowly (Text-fig. 12C2–C5).

The two modes of initiation can occur in different parts of a single corallum. The boundary between modes occurs where tabularium area is about 50–60% of corallite area. Bursts of increase are sometimes concentrated in skeletal bands showing cyclomorphically close vertical spacing of elements. Increase may be common up to the very top of a corallum.

In many coralla there are significant differences between the axis (area of vertical and subvertical growth) and the margins (area of more lateral growth). Tabulae are more broadly spaced in the axis than in the margins; thickening of elements is similar between the two areas, and cyclomorphic bands are continuous between the two (Pl. 3, fig. 8). Tabularia are closer together in the axis than in the margins in many coralla. There was more increase in the axis, so corallites there tend to have slightly smaller mean tabularium diameters. The relative dimensions of the axis and margins reflect corallum growth patterns and the shape of the growth surface. Relatively narrow margins are associated with more vertical growth that produced tall coralla with relatively small growth surfaces (Pl. 3, fig. 4). Marginal corallites in such coralla were often short-lived. Relatively wider margins occur in coralla that have broader growth forms (Pl. 3, fig. 8).

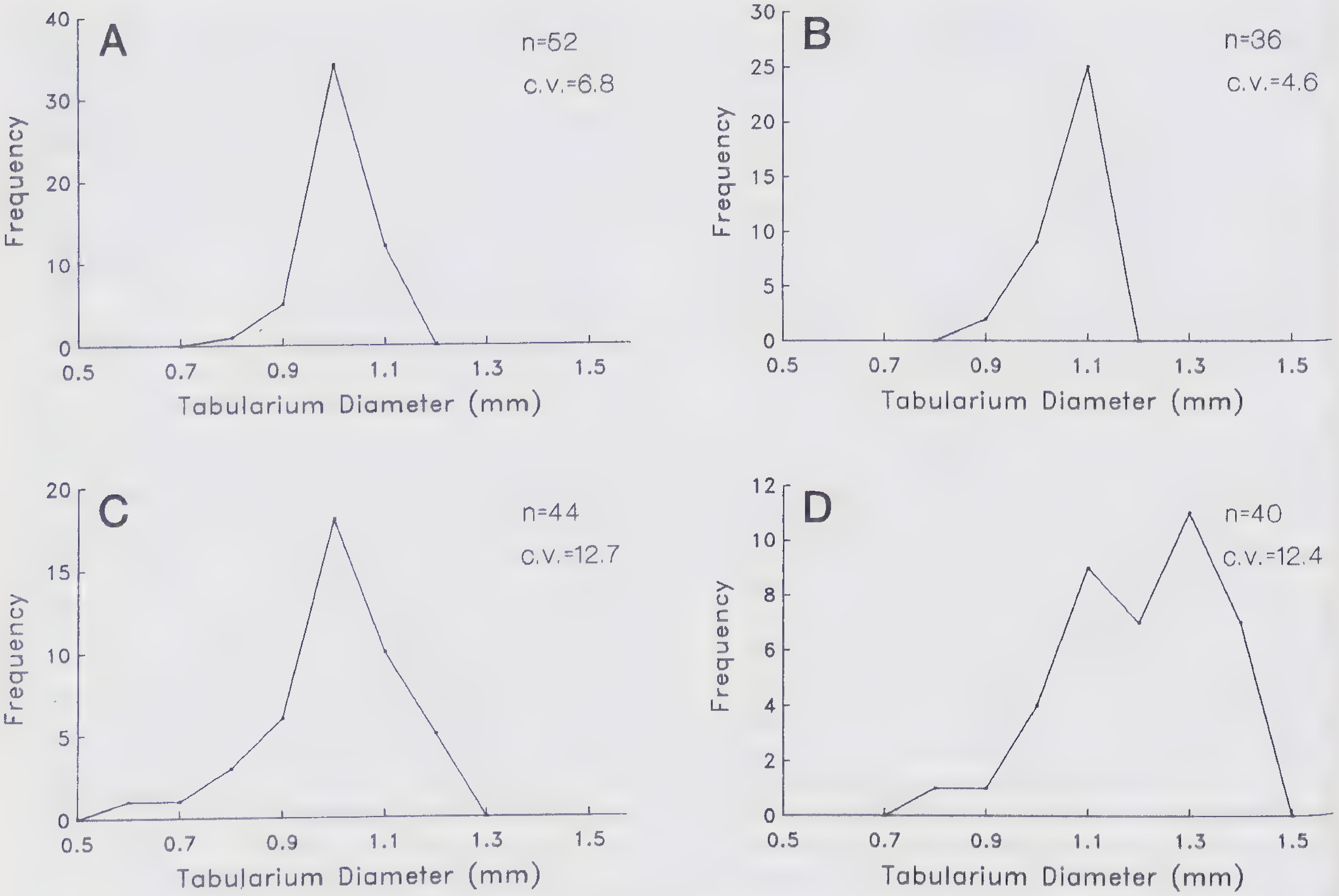
Sediment inclusions representing partial mortality of the colony surface occur in many specimens. Above these inclusions, new corallites of adult or nearly adult size were initiated across the surface of a thin holothecal layer (Pl. 2, fig. 7). These corallites are separated by coenenchymal dissepiments that are densely spaced, but of normal form. Lateral to such an inclusion, corallites in a cyclomorphically dense band may show constriction followed by rejuvenescence (Pl. 2, fig. 2, Pl. 4, fig. 3). In one corallum, the presence of an algal crust on an area of partial mortality suggests that this surface was exposed for a significant period of time prior to regeneration. Regeneration may be associated with a change in growth direction indicative of colony reorientation. Coralla were able to successfully surround and overgrow large particles deposited on their growth surfaces (Pl. 1, fig. 8).

Microstructure.—Corallite walls were produced principally by the joining together of adjacent septal trabeculae. This is most obvious where the trabeculae are thickened; the adjacent septal trabeculae commonly have thin connecting walls with which they are continuous (Pl. 1, fig. 9, Pl. 2, fig. 6). Even where septa are absent, the walls appear to be composed of trabeculae. Under polarized light, a line can be observed passing through the axes of thickened trabeculae and continuing along the wall between septa. Where the septal trabeculae are strongly thickened, the axial edges of trabeculae may be irregular and ragged, but no discrete spines are present. The trabeculae of adjacent, close-spaced corallites may coalesce without a clearly defined suture. Where corallites are closely spaced and trabeculae are thickened, pore-like structures may appear in the walls (Pl. 3, fig. 11).

Microstructure of tabulae and coenenchymal dissepiments is generally indistinct; tabulae and dissepiments are darker in color than the pale trabeculae of corallite walls (Pl. 1, fig. 9). Dissepiments are often embedded in corallite walls more deeply than are tabulae, which are attached to adaxial edges of wall trabeculae (Pl. 2, fig. 10).

Intraspecific variation.—Coralla show a high degree of variability in a number of morphologic characters, including size and spacing of tabularia, and features that are related to thickening of skeletal elements. This variability is pronounced, both within and between coralla and localities.

Tabularium size-frequency distributions show variation within and between coralla. Transverse sections from some coralla have low intracorallum variability in tabularium diameter; distributions for such specimens are unimodal, with slight negative skewness (Text-fig. 13A, B). Coralla with high intracorallum variability in tabularium diameter show two types of tabularium size-frequency distributions. Some (*e.g.*, Text-fig. 13C) are similar to the distribution seen in less variable specimens, but have a larger number of small individuals. Others show bimodal frequency distributions (Text-fig. 13D). Greater variability of tabularium diameters is most common in coralla with dense tabularium spacing and subpolygonal tabularia (*e.g.*, Pl. 3,

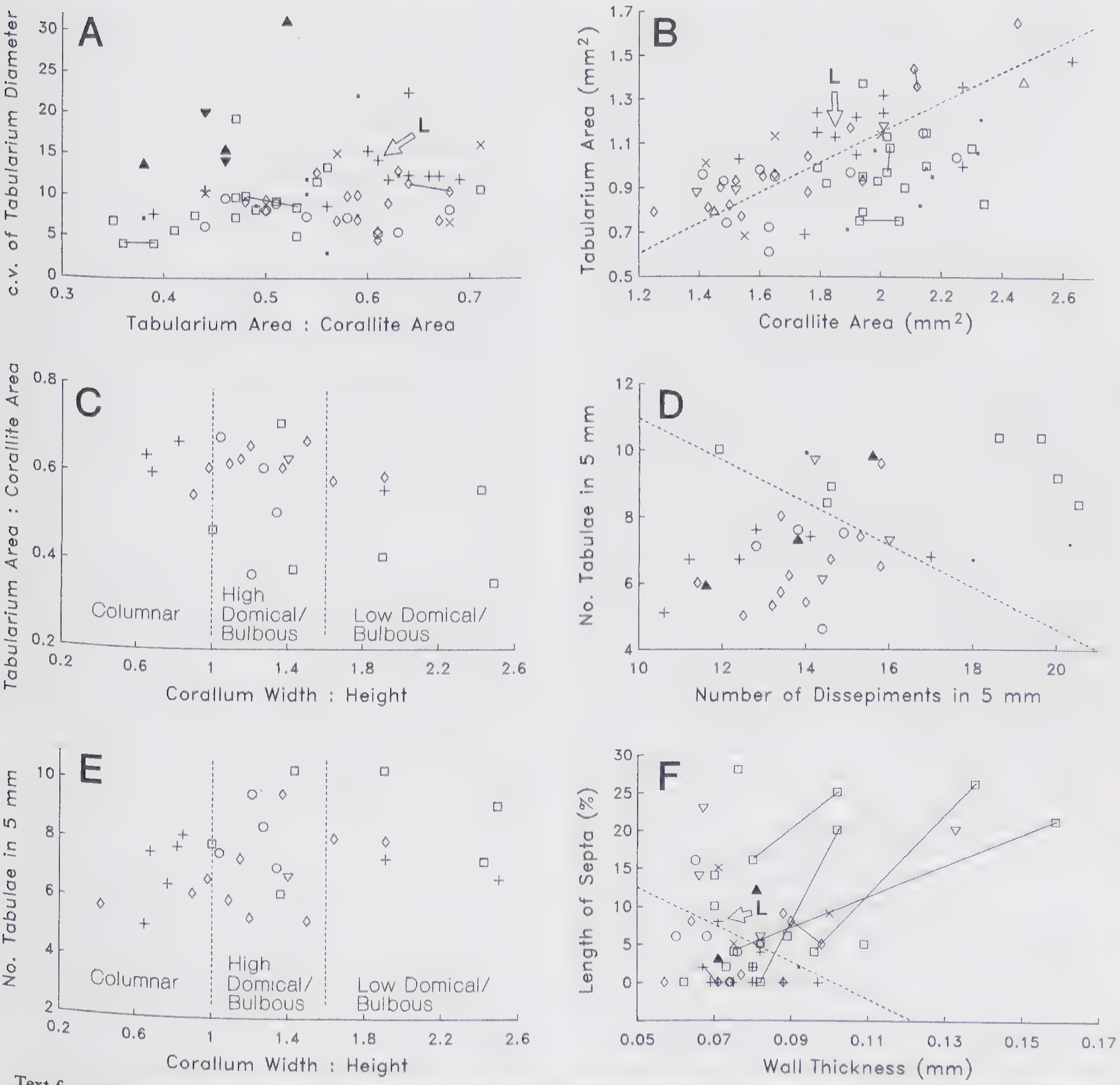


Text-figure 13.—Tabularium size-frequency distributions for selected coralla of *Propora thebesensis.* **A**, USNM 485706a, Section-interval 23-2 (Lawrence Quarry). **B**, USNM 485756, Section-interval 14-1 (Higginbotham Farm). **C**, USNM 485739, Section-interval 14-1 (Higginbotham Farm). **D**, USNM 485716, Section-interval 31-1 (Thebes North). Each graph represents a single transverse section; n = number of tabularia, c.v. = coefficient of variation.

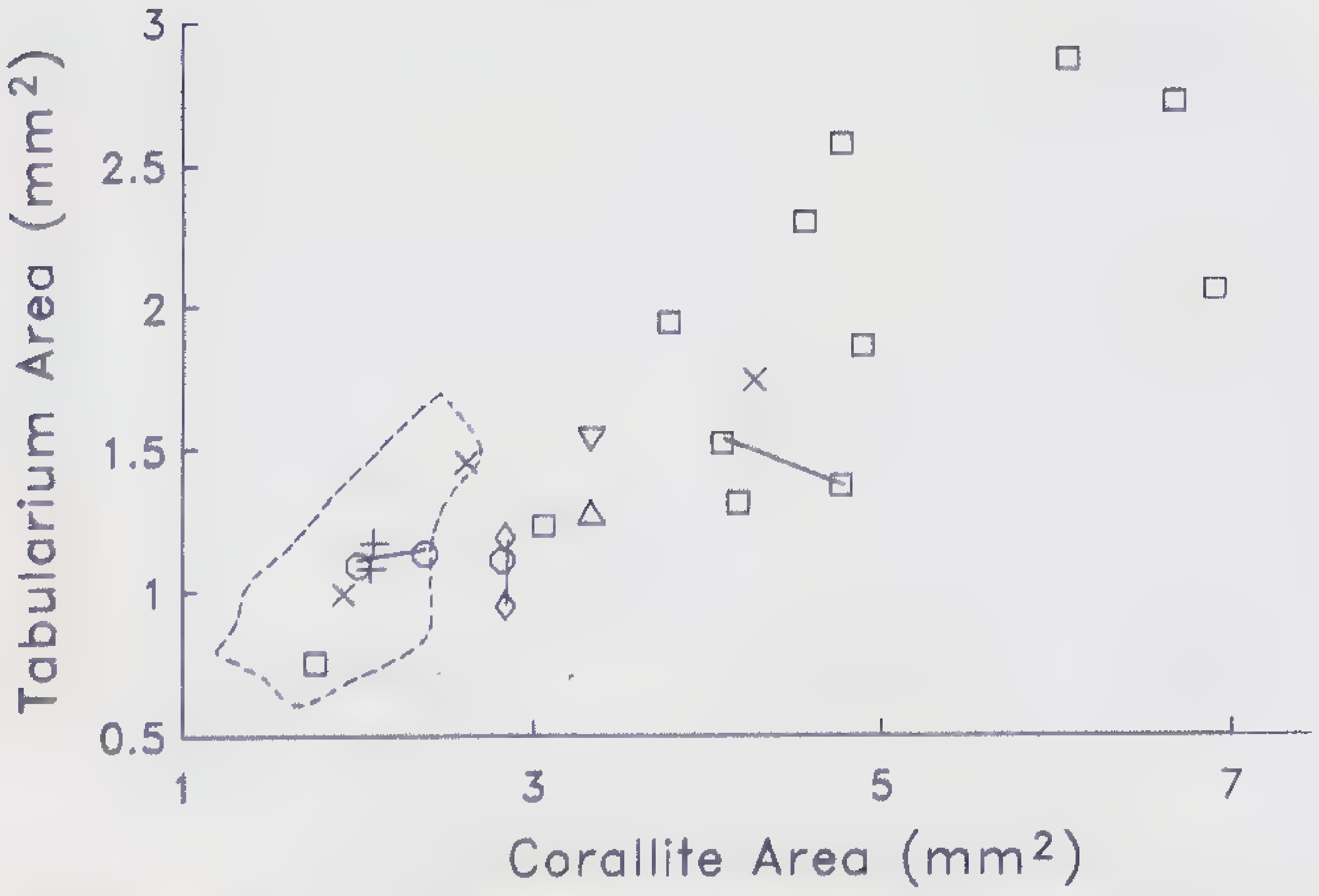
figs. 6, 9); this observation is supported by a graph of variability of tabularium diameter *versus* corallite packing for transverse sections from all measured coralla (Text-fig. 14A). This holds for intervals from which large collections were available, such as Section-interval 23-2 (Lawrence Quarry), and Section-intervals 31-1 and 31-1b (Thebes North). Specimens from two of the small collections, however, are radically different. Coralla from the Gale Section and from 5 km south of Clarksville, Missouri, have wide-spaced tabularia that are highly variable in size. Possible reasons for a general correlation between density of corallite packing and variability of tabularium diameter are considered elsewhere (see *Propora thebesensis,* p. 35).

A strong positive correlation is observed in a graph of mean tabularium area *versus* mean corallite area in transverse sections (Text-fig. 14B). This relationship is not 1:1; rather, as tabularia became larger they also tended to become more closely spaced. Specimens from each of the localities for which large collections were available show considerable variability in these features, but tend to be concentrated in one part or another of the graph. There is some evidence that these characters of size and spacing are tied to colony growth form. Those intervals in which tabularia are relatively densely spaced, such as Section-intervals 31-1 and 31-1b, and Section-interval 14-1 (Higginbotham Farm), are the ones in which taller growth forms predominate. Where tabularia are broadly spaced (Section-interval 23-2) lower forms are most common (compare Text-figs. 10 and 14B; see Tables 10, 11). The correlation between form and packing is less clear on a graph for individual coralla (Text-fig. 14C). A general trend can be distinguished, but the broad spread of points suggests that styles of growth varied (see *Astogeny and corallite increase,* above; *Growth Form,* p. 29; *P. thebesensis,* p. 35).

Vertical spacings of tabulae and of coenenchymal dissepiments show a general linear relationship (Text-fig. 14D); these characters also vary with locality and



Text-figure 14.—Intercorallum variation in morphologic characters of *Propora thebesensis* from the east-central United States. **A**, Relationship between coefficient of variation (c.v.) of tabularium diameter and density of tabularium spacing (mean tabularium area as a proportion of mean corallite area) for transverse sections from 67 coralla. **B**, Relationship between mean tabularium area and mean corallite area for transverse sections from 69 coralla. **C**, Relationship between density of tabularium spacing and generalized growth form (corallum width as a proportion of corallum height) for 24 coralla. **D**, Relationship between number of tabulae and number of dissepiments in unit 5 mm for longitudinal sections from 37 coralla. **E**, Relationship between number of tabulae in unit 5 mm and generalized growth form for 28 coralla. **F**, Relationship between length of septa as a percentage of tabularium radius and mean wall thickness for transverse sections from 47 coralla. Each data point represents a single thin section; solid lines connect sections from different parts of a single corallum; L = USNM 84863b (lectotype). Arbitrary dashed lines in B, D, and F were used to derive proportions shown in Table 11. Terms for corallum growth form in C and E are defined in *Growth Form* under *The Edgewood Colonial Corals.* Symbols for Sections and Section-intervals: □ 23-2 and 23-2a (Lawrence Quarry); + 31-1 and 31-1b (Thebes North); ▼ Gale Section; × 18-3 and 18-4 (Kissenger); ▲ 5 km south of Clarksville, Missouri; ▽ 16-1 and 16-2 (Clinton Spring); ◇ 14-1 (Higginbotham Farm); ○ 15-1 (Calumet); △ 32-1c (Thomson East); ■ all other Section-intervals.



Text-figure 15.—Comparison of selected species of *Propora:* relationship between mean tabularium area and mean corallite area on transverse sections. Data points are for individual coralla except as otherwise stated; solid lines connect thin sections from single coralla. A dashed line surrounds the field of distribution for 69 coralla of *P. thebesensis* from the east-central United States. Symbols for other species: □ *P. savagei;* east-central United States; n (number of coralla) = 11; ◇ *Propora* sp. aff. *P. affinis;* east-central United States; n = 1; ○ *P. thebesensis paucivesiculosa;* Manitoulin Formation, southern Ontario; n = 2; ▽ *P. affinis;* Gun River Formation, Anticosti Island, Québec; GSC 2340, 2340a (one syntype); + *P. conferta;* Ellis Bay Formation, Anticosti Island, Québec; the two data points represent means for specimens from Pointe Laframboise (n = 179) and all other localities (n = 59) (data from Dixon, 1974, table 3); × *P. conferta;* Grande Coupe beds, Matapédia Group, near Percé, Québec; n = 3; △ *Propora* sp. A of Bolton (1980); Honorat Group, north of Carleton, Québec; n = 1.

with growth form. Coralla from Section-intervals 31-1, 31-1b, and 14-1, where tall forms are most common, have tabulae and dissepiments with wider vertical spacings than do those from Section-interval 23-2, where lower forms are dominant (see Tables 10, 11). As was the case for packing of tabularia, this correlation is stronger when examined by locality (Text-fig. 14D) than when plotted for individual coralla (Text-fig. 14E). For further discussion on the relationship between growth form and vertical spacing of elements, see *Growth Rate* (p. 31).

Thickening of walls and development of septa are extremely variable (Text-fig. 14F). Skeletal elements in coralla from Section-interval 23-2 are commonly more strongly thickened than those in specimens from other localities. There is overlap, however, and measurements from different parts of individual specimens from Section-interval 23-2 indicate that intracolony variation can be nearly as great as the intraspecific variability.

General comparisons of characters at the major localities are presented elsewhere (see *Propora thebesensis,* p. 35).

Discussion.—Foerste (1909) based *Lyellia thebesensis* on material collected at Section 31 (Thebes North). He illustrated two coralla, which we designate as the lectotype (USNM 84863b; see Pl. 3, figs 1, 2) and paralectotype (USNM 84863a; see Pl. 3, fig. 3) of *Propora thebesensis.* The lectotype is better preserved than are most specimens from this locality, and shows a degree of cyclomorphic variation that records much of the range of intraspecific variability. Most numerical characters of this specimen are near the species mean: TaD = 1.20 mm, CoA = 1.85 mm^2, WT = 0.071 mm (thickened) and 0.058 mm (unthickened), LS = 15% (thickened) and 0% (unthickened) (compare with Table 15).

Lyellia thebesensis from the type locality was also described and illustrated by Savage (1913, 1917). The corallum he photographed (Savage, 1913, pl. 3, fig. 7; 1917, pl. 5, fig. 7) is apparently lost; the specimen labelled as Savage's hypotype (UI X-908; see Pl. 2, figs. 11, 12) is externally similar but is not identical. Many coralla that we have studied from the type locality are near one end of the spectrum of variation of *P. thebesensis* (see *Intraspecific variation,* above), but they are clearly conspecific with all other material of this species. Two other species included in this study, *Propora savagei* and *Propora* sp. aff. *P. affinis,* have some close similarities to *P. thebesensis* (see Text-fig. 15); the differences and possible relationships are discussed under those two species.

The only material previously described as *P. thebesensis* from outside the east-central United States is from the Manitoulin Formation of the Cataract Group in southern Ontario (lower Lower Silurian, Lower Llandovery, Rhuddanian; Barnes and Bolton, 1988, p. 252; Brett *et al.,* 1991, fig. 5). This material was designated as *Lyellia thebesensis paucivesiculosa* by Bolton (1957). We examined the following material: ROM 7490 (Bolton, 1957, pl. 6, fig. 4), 7491(783CL) (holotype; Bolton, 1957, pl. 6, figs. 2, 3, 5–7), upper biohermal beds, ROM 7474a(766CL), 7474b(766CL), 29542, collected by H. G. Way, Bidwell Township, Manitoulin Island, Ontario; GSC 11066 (Bolton, 1957, pl. 6, fig. 1), collected by T. E. Bolton in 1950, southeast quarry of Owen Sound, Ontario.

Bolton's holotype of *L. thebesensis paucivesiculosa* has tabularia with a mean diameter of 1.17 mm, tabularium area averaging 50% of corallite area, thin walls, and small, globose coenenchymal dissepiments. These features, and those of most other specimens of *L. thebesensis paucivesiculosa,* are consistent with characters of *P. thebesensis.* One corallum of the former (ROM 7474b), however, has slightly larger tabularia than is common in specimens from the east-central United States, and another (GSC 11066) has tabularia that are much more widely spaced (Text-fig.

15). For these reasons, material from the Manitoulin Formation is questionably considered conspecific with *P. thebesensis,* and probably represents a distinct geographic subspecies as recognized by Bolton (1957).

Propora thebesensis is a member of a group of Late Ordovician and Early Silurian species belonging to *Propora* that have similar tabularium sizes (typically in the range of 1–2 mm), septa that may have trabecular thickening but lack spines, and coenenchymes that do not have well-developed vertical rods or plates. Other members of this group have been commonly assigned to *Propora affinis* and *Propora conferta,* but the high intraspecific variability of *P. thebesensis* and the other taxa makes recognition of species boundaries difficult. It is clear that at least some of the differences between species are related to stratigraphic position and may be due to phyletic evolution, but geographic variation may also be a factor; detailed analysis of variation in other regions is needed.

Specimens that are similar to *P. thebesensis* occur in the uppermost Ordovician (Gamachian) to lower Lower Silurian (Llandovery) on Anticosti Island, Québec, in units ranging from the Ellis Bay Formation to the Chicotte Formation. These proporids have previously been assigned to either *P. affinis* or *P. conferta. Propora thebesensis* is not conspecific with the type material of either species, but it is conspecific with some specimens from Anticosti that have been assigned to both species in the past. The names *affinis* and *conferta* have long and complex histories, and a brief discussion of each is necessary so that species relationships can be put into context.

Heliolites affinis was proposed by Billings (1865) to include a variety of material of different ages from several parts of Anticosti Island. We examined a syntype (GSC 2340, 2340a) collected by J. Richardson in 1856 from about 5 km west of the mouth of Jupiter River. This specimen is from the Gun River Formation (Middle Llandovery, lower Aeronian; Barnes, 1988, fig. 2) (see Dixon, 1974, p. 578; Bolton, oral commun., 1993). It has a tall bulbous growth form, a mean tabularium diameter of 1.40 mm (measured on external surface), and tabularium area averaging 46% of corallite area. These characters are consistent with those of *P. thebesensis,* but this specimen differs from the latter species by having a larger mean corallite area of 3.33 mm^2 (see Text-fig. 15) and it appears to have broad coenenchymal dissepiments. Billings (1866) later republished his description of this species, and other early workers, including Lambe (1899) and Twenhofel (1928), used the name *affinis* and followed his concept of it as a widely occurring species on Anticosti.

Propora conferta was first described, but not illustrated, by Milne-Edwards and Haime (1851, p. 225) from Borkholm (probably Upper Ordovician, Ashgill, F_{II}, Porkuni Stage; Twenhofel, 1916, pp. 293, 306; Rõõmusoks, 1960, table 1) and Chavli, Estonia (probably not *in situ* according to Lindström, 1899, p. 93). The type specimens, as described and illustrated by Lindström (1899, pp. 93, 94, pl. 8, figs. 32–34, 37–39), differ from *P. thebesensis* by having larger tabularia with diameters of about 1.75–2.0 mm, often broad coenenchymal dissepiments, and sometimes very densely spaced tabulae. Lindström (1899, pp. 93, 94) was the first to consider *P. affinis* to be a junior synonym of *P. conferta.* The synonymization of these two species has been followed more recently by Dixon (1974) and Bolton (1981a).

The available illustrations and descriptions of *P. affinis/conferta* from Anticosti Island indicate that the older specimens, from the Ellis Bay Formation (Gamachian to possibly Lower Llandovery, lowermost Rhuddanian; Melchin *et al.,* 1991, p. 1861) and the Becscie Formation (Rhuddanian; Barnes, 1988, fig. 2), are so similar to *P. thebesensis* that they must be considered conspecific with it; changes in character that are apparently evolutionary prevent such an assignment for material from younger formations. Variation in specimens from member 7 at the top of the Ellis Bay Formation at a number of localities has been documented by Dixon (1974; unit referred to as member 6 therein). These specimens have a variety of growth forms, subcircular tabularia with a mean diameter of 1.2 mm, variable but generally close tabularium spacing with tabularium area averaging 52% of corallite area, sometimes thickened septal trabeculae, and globose coenenchymal dissepiments. Their overall range of variation is very similar to that of *P. thebesensis* from the east-central United States (see Text-fig. 15); the only difference is that tabularia in the Anticosti material are apparently never so densely spaced that they become subpolygonal.

Material identified as *P. conferta* from the Ellis Bay Formation at several localities has also been illustrated by Bolton (1981a, pl. 1, figs. 6, 7, pl. 2, figs. 6, 7, pl. 3, figs. 1, 2); it has characters consistent with those of *P. thebesensis.* The corallum illustrated by Lindström (1899, pl. 9, figs. 11, 12) from Junction Cliff is probably from the lower Ellis Bay Formation (see Barnes *et al.,* 1981, p. 8); it has somewhat wider spaced tabularia and broader coenenchymal dissepiments than is typical for *P. thebesensis.* Specimens from the overlying Becscie Formation, as illustrated by Bolton (1981a, pl. 8, figs. 13, 14), are very similar to *P. thebesensis* from the Keel Formation at Section 23 (Lawrence Quarry) (*e.g.,* USNM 458777; Pl. 1, figs. 4–9). Material has also been illustrated and described from the younger Gun River Formation, Jupiter Formation (upper Aeronian–

Telychian) and Chicotte Formation (Upper Llandovery, Telychian; Barnes, 1988, fig. 2) on Anticosti Island. This includes a syntype of *P. affinis* (GSC 2340, 2340a; see above) and the specimens of Bolton (1981a, pl. 9, fig. 1, pl. 11, figs. 1, 2); tabularia are typically larger and/or more widely spaced than those of *P. thebesensis.* Intraspecific variation in these younger units has not been analyzed in detail, however, and the illustrated material may not be typical.

Coralla identified as *P. conferta* from the Grande Coupe beds of the Matapédia Group near Percé, Québec (Upper Ordovician, Ashgill, pre-Hirnantian; Lespérance *et al.,* 1987, fig. 4), were described and illustrated by Bolton (1980; White Head Formation therein). We examined the following material: GSC 53528 (Bolton, 1980, pl. 2.4, fig. 1, pl. 2.5, fig. 7), 53529 (Bolton, 1980, pl. 2.4, figs. 2, 3), 53530 (Bolton, 1980, pl. 2.4, figs. 9, 10), collected by G. W. Sinclair in 1956, Grande Coupe, Québec. These hypotypes are very similar to *P. thebesensis* from the east-central United States. They have mean tabularium diameters of 1.12–1.36 mm, tabularium area averaging 41–56% of corallite area, thin walls, flat or slightly concave tabulae, and globose coenenchymal dissepiments. Nevertheless, since one of them has much more widely spaced tabularia than do specimens of *P. thebesensis* with comparable tabularium areas (Text-fig. 15), we consider them to be questionably conspecific with the latter. As they may be somewhat older than the United States material, they may represent a stratigraphically distinct subspecies. Bolton (1980, p. 14, pl. 2.2, figs. 1, 2) also described and illustrated a specimen identified as *Propora* sp. A, from the Upper Ordovician Honorat Group north of Carleton, Québec. We examined this corallum, collected by J. E. Béland and W. H. Poole in 1979 (GSC 53514). It is similar to *P. thebesensis,* having circular tabularia with a mean diameter of 1.27 mm, tabularium area averaging 38% of corallite area, and walls that appear to be of moderate thickness. Its poor preservation, however, makes detailed comparisons impossible.

Corals from two other areas of North America are similar to *P. thebesensis.* Stearn (1956, p. 72, pl. 6, fig. 3) identified *Lyellia affinis* from the Fisher Branch, East Arm, Cedar Lake, and possibly Atikameg formations of southern Manitoba (lower–upper Lower Silurian, upper Rhuddanian–Lower Wenlock; Johnson and Lescinsky, 1986, fig. 6). He described it as having generally smooth-walled tabularia with diameters (outside?) of about 1.5 mm; tabularia are in contact or separated by distances up to one-half their diameter. The only illustration of this material is an external view of a corallum, so it is difficult to determine more details. Laub (1979, pp. 332–343, pl. 34, figs. 2, 4) described a coral occurring in the mid-Llandovery Brassfield Formation of Ohio as *P. conferta.* It has tabularia with diameters (outside?) of 1.0–1.5 mm and some trabecular thickening of walls, but differs from *P. thebesensis* by possessing much broader coenenchymal dissepiments and having wider spacing of tabularia in some cases.

Sokolov (1950b) described and illustrated two species from the Lower Silurian of Tunguska, Siberia, that may be conspecific with *P. thebesensis. Propora conferta* var. *tunicata* and *Propora cancellatiformis* both have circular, close-spaced tabularia with diameters (outside?) of about 1.0–1.4 mm, and globose coenenchymal dissepiments. Sokolov (1950b) also described *P. conferta* from the Llandovery–Wenlock (?) of the same region. It is similar to *P. thebesensis,* but has tabularia with larger diameters (outside?) of 1.6–1.7 mm and apparently broad spacing.

Propora thebesensis may also be conspecific with *Propora* cfr. *magnifica* and *Propora yabei,* both documented by Ozaki (1934) from the Ken-niho Conglomerate of northwest Korea ("Gotlandian" according to Shimizu *et al.,* 1934, pp. 59, 60, 82; possibly Llandovery). These taxa have smooth-walled, close-spaced tabularia with diameters (outside?) of about 1.3 mm (size for *P. yabei* based on photographs), and globose coenenchymal dissepiments.

Propora multispinosa Lin and Chow (1977, pp. 182, 183, fig. 22, pl. 53, figs. 1a–d), from the Ashgill of Chekiang and Kiangsi provinces in China, has crenulate, moderately thick-walled tabularia with diameters of about 1.0–1.2 mm. It differs from *P. thebesensis* by having broader coenenchymal dissepiments and, apparently, some septal spines.

Among European species, *P. thebesensis* is similar to the following: *Propora cancellata* Lindström (1899, p. 95, pl. 9, figs. 27–30), from Borkholm, Estonia (probably Ashgill, F_{II}, Porkuni Stage; Twenhofel, 1916, pp. 293, 306; Rõõmusoks, 1960, table 1); *P. conferta* as discussed and illustrated by Lindström (1899, p. 94, pl. 9, figs. 16–22) from Dalarna (Dalecarlia in Lindström), Sweden (*Leptaena* limestone or brachiopod schists of Lindström: probably Ashgill; Jaanusson, 1963, table 2); and *P. affinis* as described and illustrated by Kiaer (1930, p. 67, pl. 4, fig. 6, pl. 5, figs. 4, 5) from Stord, Norway (possibly Upper Ordovician). *Propora cancellata* is similar to *P. thebesensis* in its smooth-walled, moderately close-spaced tabularia with diameters of about 1 mm, but has very long, platy exothecal projections that make parts of its coenenchyme look similar to that of *Plasmopora.* Lindström's *P. conferta* and Kiaer's *P. affinis* resemble *P. thebesensis* by having smooth-walled or slightly crenulate tabularia, the former with diameters of about 1.0–1.5 mm and the latter with diameters of 1.1–1.3 mm (outside?), but have wider tabularium spacing and broad, gently curved coenenchymal dissepiments.

Propora thebesensis and its probable relatives *P. affinis* and *P. conferta* bear some strong similarities to two important younger species, *Propora exigua* (Billings) and *Propora tubulata* (Lonsdale). *Propora exigua,* which was recently described and discussed by Scrutton and McCurry (1987, p. 61, figs. 2d, 2e) and by Young and Noble (1990b, pp. 191, 193, table 2, figs. 2, 5.6–5.11, 6.1), is characteristic of the Telychian in northern Europe and eastern North America. It differs from members of the *thebesensis* group by having significantly smaller tabularia (diameters of 0.4–0.9 mm) that are much more broadly spaced, but is otherwise very similar to these species and is almost certainly descended from one of them. *Propora tubulata* is widespread in Europe and eastern North America, from the lower Lower Silurian (Upper Llandovery) to the lower Upper Silurian (Ludlow) (see Young and Noble, 1990b, pp. 188, 190, 191, table 1, figs. 2, 5.1–5.6; Scrutton, 1993). It is distinguished from *P. thebesensis* by its thick, commonly abundant septal spines. Its characters also suggest descent from a member of the *thebesensis* group.

Occurrences.—Uppermost Ordovician (Gamachian): lower Keel Formation, south-central Oklahoma; Leemon Formation, southern Illinois. Uppermost Ordovician (Gamachian) to lowermost Silurian (?; Lower Llandovery?, lower Rhuddanian?): Cyrene Formation, northeastern Missouri. Uppermost Ordovician (?; Gamachian?) to lowermost Silurian (Lower Llandovery, lower Rhuddanian): Wilhelmi Formation, northeastern Illinois. Uppermost Ordovician (?; Gamachian?) to lower Lower Silurian (Lower Llandovery, upper Rhuddanian): lower and upper Mosalem Formation, northwestern Illinois. Lowermost Silurian (?; Lower Llandovery?, lower Rhuddanian?): Kissenger Limestone Member, Bryant Knob Formation, northeastern Missouri.

Uppermost Ordovician (Gamachian) to lower Lower Silurian (Lower Llandovery, Rhuddanian): Ellis Bay and Becscie formations, Anticosti Island, Québec. Possibly in Upper Ordovician (Ashgill, pre-Hirnantian): Grande Coupe beds, Matapédia Group, near Percé, Québec. Possibly in lower Lower Silurian (Lower Llandovery, Rhuddanian): Manitoulin Formation, Manitoulin Island and Owen Sound area, Ontario.

Lectotype.—Designated here: USNM 84863b (Foerste, 1909, pl. 4, fig. 69b; Pl. 3, figs. 1, 2), collected by A. F. Foerste (labelled "*Lyellia thebesensis,* Brassfield [Formation], 1 mi. N. of Thebes"), Leemon Formation, Section 31 (Thebes North), Alexander County, Illinois.

Paralectotype.—Designated here: USNM 84863a (Foerste, 1909, pl. 4, fig. 69a; Pl. 3, fig. 3), collected by A. F. Foerste (labelled "*Lyellia thebesensis,* Brassfield [Formation], 1 mi. N. of Thebes"), Leemon Formation, Section 31 (Thebes North), Alexander County, Illinois.

Other material described above.—87 specimens: USNM 459087, 485700, site 23i, USNM 485701–485703, site 23ii, USNM 458777, 459075, 485704, 485705, 485706a, 485706b, site 23iii, interval 23-2 (*Brevilamnulella* beds), USNM 485707–485709, site 23i, interval 23-2a, Keel Formation, Section 23 (Lawrence Quarry), Pontotoc County, Oklahoma; UI X-908, C-1437d, collected by T. E. Savage (labelled "*Lyellia thebesensis,* Edgewood [Formation], near Thebes"), UI C-3085a, collected by T. E. Savage (labelled "*Lyellia thebesensis,* Edgewood [Formation], Thebes"), USNM 459083, 485710–485718, interval 31-1, USNM 485719–485721, interval 31-1b, Leemon Formation, Section 31 (Thebes North), Alexander County, Illinois; UI C-1358, collected by T. E. Savage (labelled "*Favosites* cf. *venustus* with *Heliolites,* Sexton Creek [Limestone], Alexander Co.," but lithology and coral are characteristic of Leemon Formation at Section 31), probably Leemon Formation, Section 31 (Thebes North), Alexander County, Illinois; UI C-880, C-886a, collected by T. E. Savage (labelled "*Lyellia thebesensis,* Edgewood [Formation], near Gale"), Leemon Formation, Gale Section, Alexander County, Illinois; USNM 485722, 485723a, 485723b, 485724, interval 18-3, USNM 459084, interval 18-4, Kissenger Limestone Member, Bryant Knob Formation, Section 18 (Kissenger), Pike County, Missouri; UI C-1462a, C-1462c, collected by T. E. Savage (labelled "*Lyellia thebesensis,* Edgewood [Formation], 3 mi. S. Clarksville"), UI C-1466b, collected by T. E. Savage (labelled "*Favosites subelongus,* Edgewood Ls., 3 mi. S. Clarksville"), Bryant Knob Formation, 5 km south of Clarksville, Pike County, Missouri; USNM 459077, interval 16-1, USNM 459076, 485725, 485726, interval 16-2, Kissenger Limestone Member, Bryant Knob Formation, Section 16 (Clinton Spring), Pike County, Missouri; USNM 485727a, 485728–485738, interval 15-1, Kissenger Limestone Member, Bryant Knob Formation, Section 15 (Calumet), Pike County, Missouri; USNM 485739–485757, interval 14-1, Kissenger Limestone Member, Bryant Knob Formation, Section 14 (Higginbotham Farm), Pike County, Missouri; UI C-865a, C-865c, C-865d, C-865f, collected by T. E. Savage (labelled "*Lyellia thebesensis,* Edgewood [Formation], Edgewood"), Cyrene Formation, near Edgewood, Pike County, Missouri; UI C-1590, collected by T. E. Savage (labelled "*Lyellia thebesensis,* 1 mi. below Channahon ls. otc."), Wilhelmi Formation, 3.2 km south of Channahon, Will County, Illinois; USNM

485758, interval 32-1z, USNM 485759–485763, interval 32-1c, Mosalem Formation, Section 32 (Thomson East), Carroll County, Illinois.

Propora savagei, new species
Plate 5, figures 1–10; Plate 6, figures 1–4

Derivation of name.—The species name honors T. E. Savage, who did important early work on the uppermost Ordovician and lowermost Silurian in the east-central United States, and who collected many of the specimens described here.

Diagnosis.—*Propora* with crenulate tabularia having pronounced exothecal projections; adult tabularium diameter usually 1.0–2.0 mm, tabularium area about 30–50% of corallite area. Septa have thickened bases and spinose adaxial extensions; other distinct trabeculae commonly occur between septal trabeculae in walls. Coenenchymal dissepiments broad.

Description of coralla.—Coralla are most commonly of high bulbous growth form, rarely low bulbous or columnar (Table 14). Most are very small; measured specimens are 10–19 mm wide and 11–19 mm high.

In transverse section, tabularia are usually crenulate (Pl. 5, figs. 5, 9, Pl. 6, fig. 1), rarely smooth-walled (Pl. 5, fig. 8); pronounced exothecal projections are common (Pl. 5, figs. 7, 9). Adult tabularia commonly have diameters of 1.0–2.0 mm (Table 15). Tabularia are closely spaced, tabularium area is usually 30–50% of corallite area (Table 15); spacing is rarely so close that tabularia are compressed into subpolygonal shapes. In longitudinal section, tabularia are generally straight or gently curved, more strongly curved in lateral parts of each corallum (Pl. 6, fig. 2).

Corallite walls are thick, commonly 0.10–0.20 mm (Table 15). Walls are slightly thickened at septa in some specimens. Trabeculae from which pointed or ragged exothecal projections are developed occur at or between septa (Pl. 5, fig. 7, Pl. 6, fig. 3). Septa number 12, with basal ridges having variably developed, upwardly directed spines. Spines may be thick and square-ended (Pl. 5, fig. 5), slender (Pl. 6, figs. 3, 4), or slightly ragged (Pl. 5, fig. 3). Septal length is usually 20–30% of tabularium radius (Table 15). In a few coralla, septal spines are rare (Pl. 5, figs. 7, 9, 10).

Tabulae are of medium thickness, flat, slightly to strongly concave (Pl. 5, fig. 2) or slightly convex. They are usually complete (Pl. 5, figs. 4, 10), but are rarely incomplete (Pl. 6, fig. 2). Tabulae are usually wide-spaced, averaging about seven in 5 mm (Table 15); dense spacing is rare (Pl. 5, fig. 2). Tabular spacing shows cyclomorphic variation in some cases (Pl. 6, fig. 2). A single tabula may have variable thickness between axial and lateral parts; spines rarely project from the upper surfaces of thickened tabulae (Pl. 5, fig. 6).

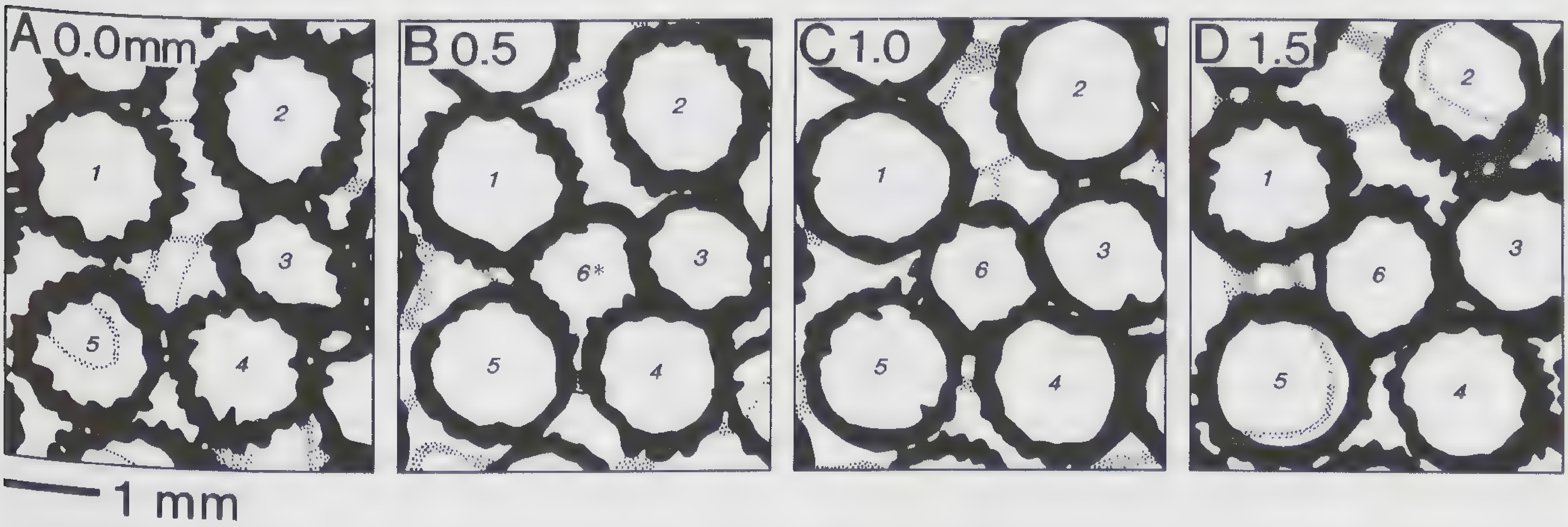
In longitudinal section, coenenchyme is usually composed of broad, flattened dissepiments (Pl. 5, figs. 4, 10), averaging about 13 in 5 mm (Table 15). Dissepiments are about twice as numerous as corallite tabulae in a unit of vertical distance (Table 15). Dissepiments are extremely broad in some coralla (Pl. 5, fig. 10), but where tabularia are closer together, dissepiments are more globose or appear as flat plates. Coenenchymal thickening is variable; dissepiments are more commonly thickened near corallite walls, but some also show a degree of cyclomorphic thickening (Pl. 6, fig. 2). Dissepiments commonly bear short, node-like structures on their upper surfaces (Pl. 5, figs. 4, 6, 10). These structures usually consist of the outer parts of exothecal wall projections, but in some coralla rare vertical rods or spines occur in the coenenchyme (Pl. 5, fig. 10). Dissepiments appear as sparsely distributed plates in transverse section.

Astogeny and corallite increase.—A single, serial-sectioned corallum (USNM 485766) is the basis for detailed observation. Other specimens are used for comparison.

The absolute base of the corallum is unknown. Close to the base, thick-walled corallites occur in a small group, with moderately close spacing. During subsequent growth, this group of axial corallites became slightly wider-spaced. There is some vertical variation in spacing and thickening of elements with height in the corallum, but these characters do not change in any consistent way in the transition from basal to subsequent growth. There is no evidence that growth patterns changed near the end of each colony's life. Corallites commonly extend through much of the height of a corallum.

Corallite increase is coenenchymal. In most examples, tabularia that are of nearly adult size were initiated on the upper surfaces of flattened coenenchymal dissepiments (Text-fig. 16A, B; Pl. 5, figs. 6, 10, Pl. 6, fig. 2). These new tabularia expanded rapidly (Text-fig. 16B–D). In transverse section, new tabularia initiated in such settings are not easily distinguished from adult tabularia. Corallite initiation between more densely spaced adult tabularia is much rarer than in *Propora thebesensis* (see *Astogeny and corallite increase* under *Propora thebesensis,* p. 49). In such cases the base of each initiate shows a gradual transition in character of horizontal elements, from coenenchymal dissepiments to tabulae. New tabularia in close-spaced settings expanded more slowly and may be subpolygonal in transverse section. Most increase was spread through the vertical growth of the corallum, but bursts of concentrated increase do occur in certain horizontal bands.

Growth of most coralla was largely vertical. Corallite



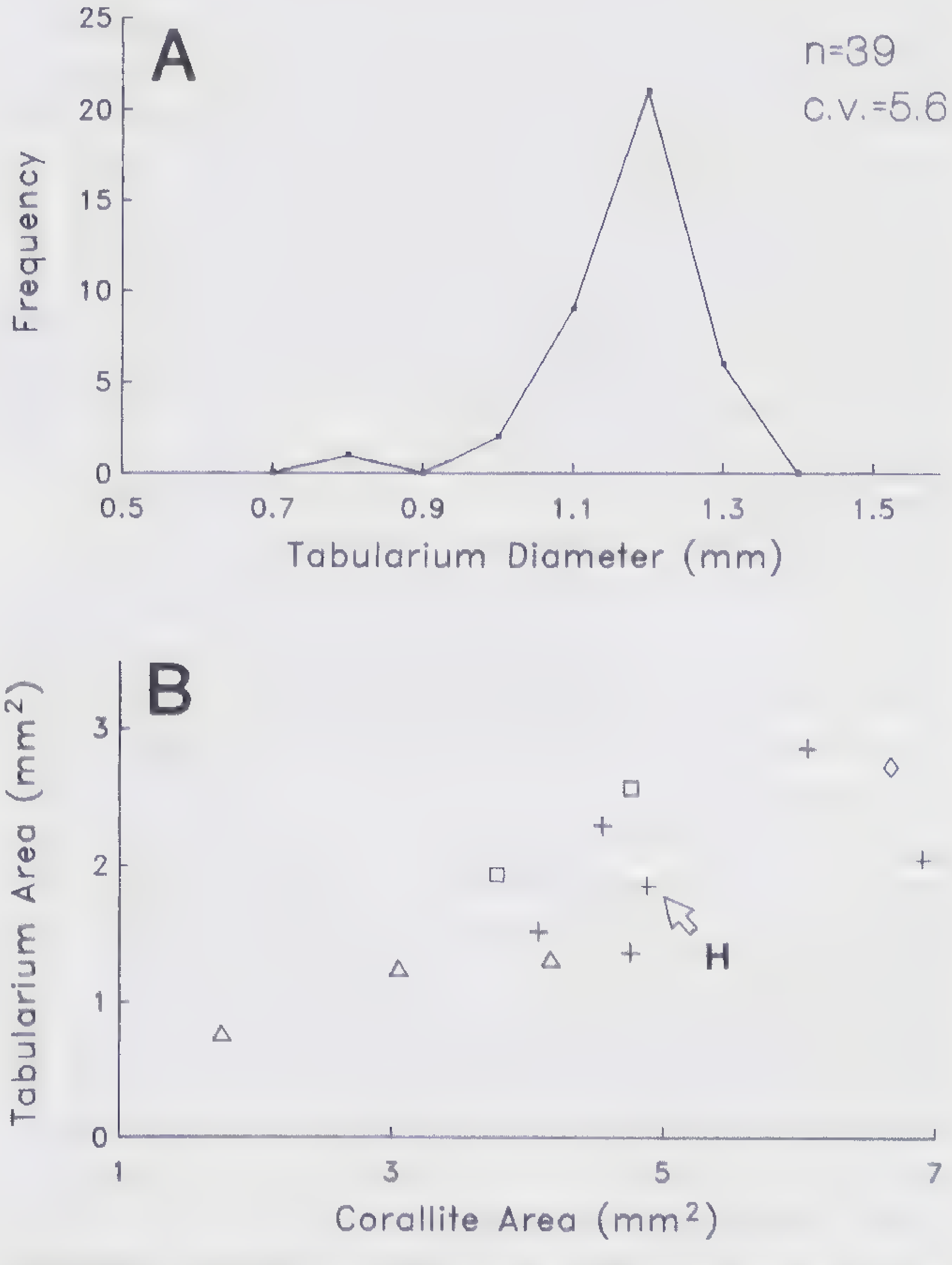
Text-figure 16.—**A–D**, Serial transverse sections illustrating corallite increase in a corallum of *Propora savagei;* USNM 485766 (paratype), Section-interval 20-6 (Short Farm) (see also Pl. 5, figs. 7–10). Corallite walls and septa are solid, tabulae and dissepiments are stippled; scale bar is shown. Heights in mm are above an arbitrary datum within a mature, axial part of the corallum; numbers in italics represent individual corallites; the asterisk beside *6* in B indicates the first appearance of that corallite.

divergence in such coralla is slight, but spacing of corallites is somewhat denser in the corallum axis than in the margins. Vertical spacing of tabulae is broader in the axis than the margins (Pl. 6, fig. 2). Cyclomorphic variation in thickening of elements is subtle, but bands appear to extend across the entire corallum.

Areas representing partial mortality of the growth surface occur in some coralla. New corallites of nearly adult size were initiated across the upper surface of a thin holotheca occurring above such an area. Corallites immediately lateral to areas of partial mortality sometimes show marked constriction followed by rejuvenation (Pl. 5, fig. 6). Regeneration is sometimes associated with a changed direction of growth indicative of reorientation during colony growth.

Microstructure.—Corallite walls are trabecular; a trabecula occurs at the base of each septum, but in most corallites other trabeculae between these give the walls their thickened appearance (Pl. 5, fig. 7). In some corallite walls, a total of 19 or 20 trabeculae can be recognized in transverse section. Exothecal projections may be developed from all trabeculae in a wall, and thus occur both at and between septa (Pl. 5, fig. 9). Tabulae are embedded in adaxial edges of wall trabeculae, while coenenchymal dissepiments are embedded deeper in the wall (Pl. 5, fig. 3).

Intraspecific variation.—Since relatively few coralla are known, many aspects of intraspecific variation cannot be analyzed in detail. The frequency distribution of tabularium size for one corallum is close to a normal distribution, but with slight negative skewness (Text-fig. 17A). Tabularium area and corallite area show a strong positive correlation (Text-fig. 17B). There seem to be distinctions among localities for these characters,



Text-figure 17.—Intraspecific variation in *Propora savagei.* **A**, Tabularium size-frequency distribution for a transverse section; USNM 485766 (paratype), Section-interval 20-6 (Short Farm). n = number of tabularia, c.v. = coefficient of variation. **B**, Relationship between mean tabularium area and mean corallite area for transverse sections; H = UI X-8722 (holotype). Symbols for Section-intervals: □ 23-3 (Lawrence Quarry); n (number of coralla) = 2; + 31-1 and 31-1b (Thebes North); n = 6; △ 20-1 and 20-6 (Short Farm); n = 3; ◇ 14-1 (Higginbotham Farm); n = 1.

but because most coralla are small, absolute measurements of size and spacing of internal features should be interpreted with some caution. In relative terms, the two coralla from the Keel oölite in Section-interval 23-3 (Lawrence Quarry) have more closely spaced tabularia than do those from other localities, such as Section-intervals 31-1 (Thebes North) and 20-6 (Short Farm).

Morphologic characters of this species generally show little or no variation between most localities; these features include tabularium diameter, form of septa, appearance of coenenchymal dissepiments and tabulae, and patterns of thickening of elements. The only important differences are those between the three specimens from Section 20 (Short Farm) and coralla from all other localities (see *Discussion,* below).

Discussion.—These coralla are assigned to a new species, *Propora savagei.* This species has close affinities with *Propora thebesensis,* but is recognized as distinct on the basis of its usually larger and more widely spaced tabularia (Text-fig. 15), thicker walls, broad and flattened coenenchymal dissepiments, and common occurrence of thickened wall trabeculae between septa. It probably evolved from *P. thebesensis,* or from a closely related older coral such as *Propora conferta* as described and illustrated by Bolton (1980, p. 20, pl. 2.4, figs. 1–3, 9, 10, pl. 2.5, fig. 7) from the Grande Coupe beds of the Matapédia Group near Percé, Québec (Upper Ordovician, Ashgill, pre-Hirnantian; Lespérance *et al.,* 1987, fig. 4) (see *Discussion* under *P. thebesensis,* p. 54).

A few coralla from Section 20 (Short Farm) are especially similar to *P. thebesensis* in several characters, including tabularium diameter, form of coenenchyme, and thickening of corallite walls. These are among the oldest specimens of *P. savagei,* and may have belonged to a transitional population. *Propora savagei* occurs only in the east-central United States and is not known from north of northeastern Missouri. It is generally found in strata that were probably deposited under high-energy conditions, such as Section-intervals 23-3 (Lawrence Quarry), 31-1 (Thebes North), and 14-1 (Higginbotham Farm). This species may thus represent a specialized local variant belonging to the *thebesensis* group. *Propora savagei* was referred to as *Propora* n. sp. aff. *P. thebesensis* by Elias and Young (1992, fig. 2, tables 1, 2).

Propora savagei is somewhat similar to *Propora speciosa,* which is also found in uppermost Ordovician to lowermost Silurian rocks of the east-central United States. *Propora speciosa,* however, has much larger tabularia (diameters commonly 2–3 mm), common or abundant rods in the coenenchyme, and longer, thicker, more abundant septal spines (Pl. 6, figs. 5–10, Pl. 7, figs. 1–8; see under *P. speciosa,* p. 59). *Propora* sp. aff. *P. speciosa* of Bolton (1981a, pl. 11, figs. 3, 4), from the Jupiter Formation on Anticosti Island, Québec (lower Lower Silurian, Middle–Upper Llandovery, upper Aeronian–Telychian; Barnes, 1988, fig. 2), has tabularia that are just slightly larger than those of *P. savagei.* It is differentiated from the latter by its irregular and incomplete tabulae that often have their upper surfaces covered with small spinules, and by its weaker septal thickenings and apparent lack of septal spines.

Occurrences.—Uppermost Ordovician (Gamachian): lower Keel Formation, south-central Oklahoma; Leemon Formation, southern Illinois and southeastern Missouri. Uppermost Ordovician (Gamachian) to lowermost Silurian (?; Lower Llandovery?, lower Rhuddanian?): Cyrene Formation, northeastern Missouri. Lowermost Silurian (?; Lower Llandovery?, lower Rhuddanian?): Kissenger Limestone Member, Bryant Knob Formation, northeastern Missouri.

Holotype.—UI X-8722 (Pl. 5, figs. 5, 6), collected by T. E. Savage (labelled "*Lyellia thebesensis,* Edgewood [Formation], Thebes, Illinois"), Leemon Formation, Section 31 (Thebes North), Alexander County, Illinois.

Paratypes.—Three specimens: USNM 485764 (Pl. 5, figs. 1–3), site 23ii, interval 23-3, Keel Formation, Section 23 (Lawrence Quarry), Pontotoc County, Oklahoma; USNM 485765 (Pl. 6, figs. 1, 2), interval 20-1, USNM 485766 (Pl. 5, figs. 7–10), interval 20-6, Leemon Formation, Section 20 (Short Farm), Cape Girardeau County, Missouri.

Other material described above.—12 specimens: USNM 485767, 485768, site 23i, interval 23-3, Keel Formation, Section 23 (Lawrence Quarry), Pontotoc County, Oklahoma; UI C-1437b, C-1437c, collected by T. E. Savage (labelled "*Lyellia thebesensis,* Edgewood [Formation], near Thebes"), USNM 485769, 485770a, 485771, 485772, interval 31-1, USNM 485773, interval 31-1b, Leemon Formation, Section 31 (Thebes North), Alexander County, Illinois; USNM 485774, interval 20-6, Leemon Formation, Section 20 (Short Farm), Cape Girardeau County, Missouri; USNM 485775, interval 14-1, Kissenger Limestone Member, Bryant Knob Formation, Section 14 (Higginbotham Farm), Pike County, Missouri; UI C-865e, collected by T. E. Savage (labelled "*Lyellia thebesensis,* Edgewood [Formation], Edgewood"), Cyrene Formation, near Edgewood, Pike County, Missouri.

Propora speciosa (Billings, 1865)

Plate 6, figures 5–10; Plate 7, figures 1–8

Heliolites speciosus Billings, 1865, pp. 426, 427; 1866, pp. 30, 31, fig. 13.

Propora speciosa (Billings, 1865). Lindström, 1899, pp. 95, 96 [par-

tim], pl. 9, figs. 40–42 [*non* pl. 9, figs. 43–46, pl. 10, figs. 1–5]; Dixon, 1974, pp. 580–583, figs. 7, 8, pl. 3, figs. 1–10; Bolton, 1981a, pl. 2, fig. 5.

Propora (*Pinacopora*) *girvanensis* (Nicholson and Etheridge, 1880). Lindström, 1899, pl. 9, figs. 36–39.

Pinacopora grayi Nicholson and Etheridge, 1878. Lindström, 1899, p. 99.

Lyellia americana Milne-Edwards and Haime, 1851. Lambe, 1899, pp. 85, 86 [*partim; non* pl. 5, figs. 2, 2a].

Calvinia edgewoodensis Savage, 1913, p. 66, pl. 12, figs. 15–17; 1917, p. 116, pl. 4, figs. 15–17.

Cavella edgewoodensis (Savage, 1913). Stechow, 1922, pp. 152, 153.

Lyellia speciosa (Billings, 1865). Twenhofel, 1928, p. 135.

[*cf.*] *Propora magna* Sokolov, 1955, pl. 78, figs. 1, 2; 1962, pl. 5, figs. 2a, 2b.

[?] *Propora speciosa* (Billings, 1865). Bolton, 1980, p. 20, pl. 2.5, figs. 1, 3, 6; Bondarenko and Minzhin, 1981, pp. 7–12, figs. 1–3, pl. 1, figs. 1–4, pl. 2, figs. 1–4.

Diagnosis.—*Propora* with crenulate tabularia; adult tabularium diameters about 2–3 mm, tabularium areas about 25–50% of corallite areas. Thickened septal bases commonly bear thick spines; distinct trabeculae commonly occur between septal trabeculae in corallite walls. Thick trabecular rods pass vertically through small, globose coenenchymal dissepiments.

Description of coralla.—Growth form can be determined for only two specimens. One (UI X-850) is of high bulbous form, 76 mm wide and 53 mm high; the other (UI C-1438) is high domical, 82 mm wide and 48 mm high.

In transverse section, tabularia are circular or subcircular, and markedly crenulate in outline (Pl. 7, figs. 1, 8); short exothecal projections are rare to common (Pl. 7, figs. 1, 3, 7). Adult tabularia commonly have diameters of 2.0–2.8 mm (Table 15). Tabularia are moderately closely spaced, but walls of adjacent corallites are never in contact. Tabularium area is usually about 30% of corallite area (Table 15). In longitudinal section, tabularia are straight or slightly curved.

Walls are thick, commonly 0.15–0.25 mm (Table 15), with greater thickening at septal bases. Most thickening occurs on inner edges of walls. Walls appear to be incomplete in places. Septa are often long (Pl. 6, fig. 8, Pl. 7, figs. 1, 3), about 55–75% of tabularium radius (Table 15). Thickened septal bases bear thick, common to abundant spines that are angled upwards (Pl. 6, figs. 7, 10). Thickening of walls and development of septa may both vary cyclomorphically.

Tabulae are thin, complete or incomplete, and flat, wavy, or concave (Pl. 6, fig. 10, Pl. 7, fig. 2). They are variably spaced, averaging about five in 5 mm (Table 15). Spacing of tabulae can show distinct cyclomorphic variation, but thickness does not seem to vary significantly (Pl. 7, fig. 2). Pairs of densely spaced and widely spaced bands in one measured corallum average 7.3 mm in thickness. Incomplete tabulae are more common in bands where spacing is dense.

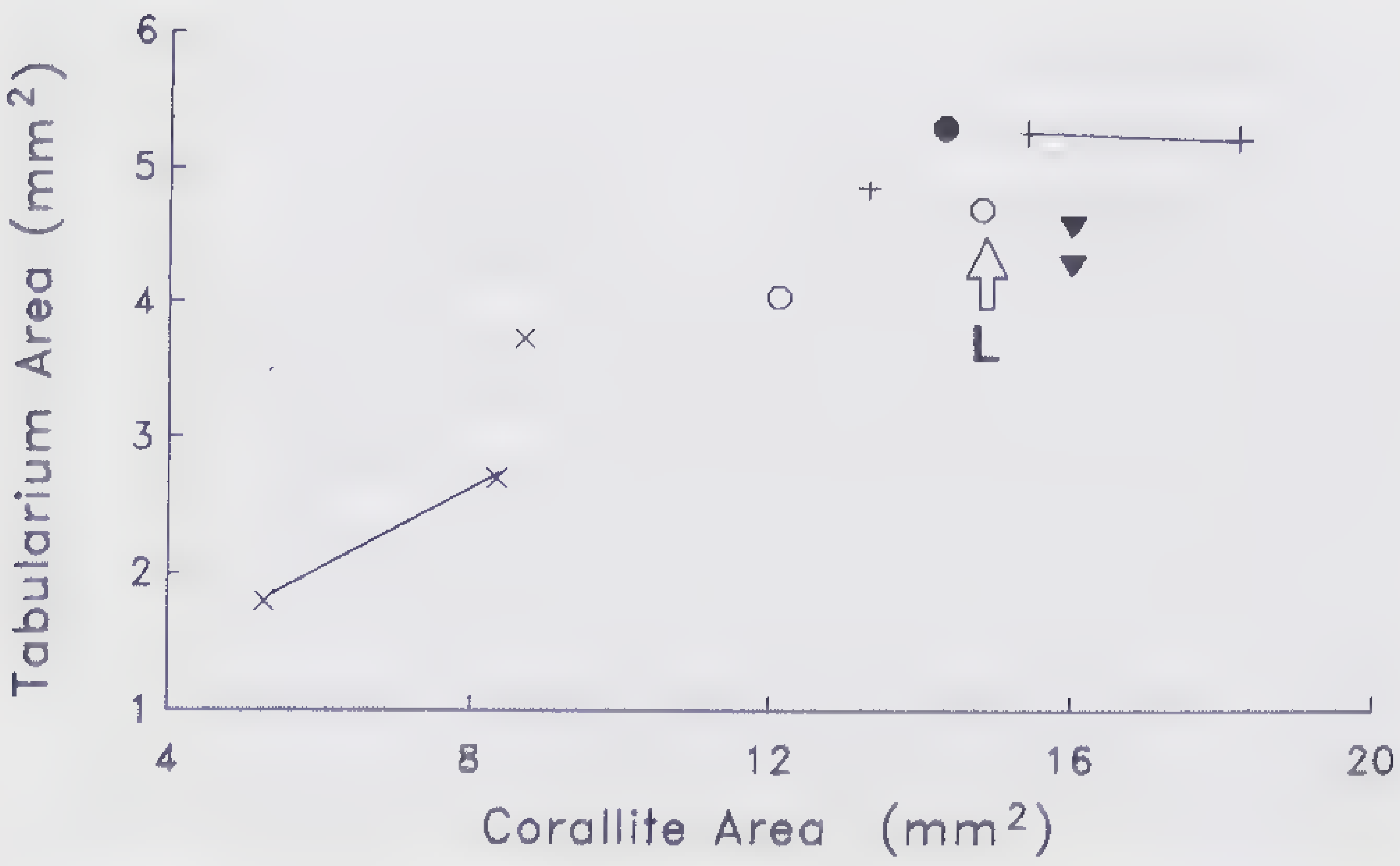
In longitudinal section, coenenchyme is composed of small, globose, moderately regular dissepiments. Dissepiments are wide-spaced, averaging about nine in 5 mm; ratio of corallite tabulae to dissepiments per unit of vertical distance is about 0.6 (Table 15). Spacing and thickening of dissepiments show some cyclomorphic variation (Pl. 7, fig. 2). Vertical skeletal elements are common to abundant in coenenchyme; these most commonly take the form of thick trabecular rods 0.125–0.225 mm in diameter and several mm long. These rods are oriented parallel to wall trabeculae and pass through coenenchymal dissepiments (Pl. 6, fig. 10, Pl. 7, fig. 5). Vertical elements may also occur as small tubercles on the upper surfaces of dissepiments (Pl. 7, fig. 2). In transverse section, coenenchymal dissepiments are thin and sparsely distributed; rods are regularly distributed between corallite walls (Pl. 7, figs. 1, 8).

Astogeny and corallite increase.—The basal parts of coralla are unknown. Preservation does not permit comparison of axial and marginal parts.

Corallite increase is coenenchymal. Tabularia that are often strongly crenulate and of nearly adult size were initiated on the upper surfaces of coenenchymal dissepiments (Pl. 6, fig. 10). In some cases, coenenchymal rods occurring below the corallite are extended upwards into wall trabeculae (Pl. 6, fig. 10, Pl. 7, fig. 2).

A sediment inclusion representing partial colony mortality occurs in a single corallum (Pl. 6, fig. 9). Above the inclusion, new corallites of nearly adult size were initiated across the upper surface of a thin holotheca. Coenenchymal trabeculae also extend upward from the holotheca, occurring in a coenenchyme of normal appearance.

Microstructure.—Corallite walls are trabecular; a trabecula occurs at the base of each septum, and other trabeculae occur in the wall between the septa. Usually one or two trabeculae occur between each pair of septal trabeculae (Pl. 7, figs. 3, 4), but three trabeculae are occasionally observed. Walls sometimes appear incomplete, with spaces occurring laterally between trabeculae (Pl. 7, fig. 7), but this may be a preservational feature. Exothecal projections may be developed from trabeculae located at any position in the wall. The trabecular rods in the coenenchyme are subcircular or irregular in transverse section and are almost radially symmetrical (Pl. 6, fig. 8, Pl. 7, figs. 3, 8); they are very similar in appearance to wall trabeculae. In some places the two types merge vertically or laterally, suggesting that they are homologous structures (Pl. 6, fig. 10, Pl. 7, fig. 2). Thick septal spines extend adaxially from the



Text-figure 18.—Relationship between mean tabularium area and mean corallite area in *Propora speciosa* (and probable synonyms) from several regions. Each data point represents a single transverse thin section, except as otherwise stated; solid lines connect sections from different parts of a single corallum. Symbols for Section-interval and other occurrences: + 31-1 (Thebes North); n (number of coralla) = 2; ▼ Gale Section; n = 2; ○ Ellis Bay Formation, Anticosti Island, Québec; GSC 2240a (L = lectotype), 2240 (paralectotype); n = 2; ● Ellis Bay Formation, Anticosti Island, Québec; mean for 46 coralla (data from Dixon, 1974, table 4); × Grande Coupe beds, Matapédia Group, near Percé, Québec; n = 2.

wall trabeculae; they are fibrous and are continuous with the fibers of the trabeculae. In some cases septal tips are downcurved (Pl. 6, fig. 10). Tabulae are embedded in the innermost edges of wall trabeculae and in some cases are suspended from septal spines (Pl. 6, fig. 10). Coenenchymal dissepiments are embedded somewhat deeper in the wall trabeculae (Pl. 6, fig. 7). Microstructure of tabulae and dissepiments can not be determined.

Intraspecific variation.—The five specimens from the east-central United States are remarkably consistent with one another in characters that are analyzed numerically. These include tabularium and corallite areas, wall thickness, septal development, and spacing of tabulae and dissepiments. On a graph of tabularium area *versus* corallite area (Text-fig. 18), the difference in corallite area between sections from a single corallum (UI C-889a) is almost as great as the overall variation for all plotted specimens from the east-central United States. Obvious differences in appearance between the studied specimens are largely due to variation in the degree and pattern of thickening of skeletal elements (*e.g.*, compare Pl. 6, fig. 10, with Pl. 7, fig. 2; see *Propora speciosa*, p. 38).

Discussion.—*Propora speciosa* was first described by Billings (1865, 1866) from member 2 of the lower part of the Ellis Bay Formation on Anticosti Island, Québec (uppermost Ordovician, Gamachian; Barnes, 1988, fig. 2) (see Dixon, 1974, p. 582). We examined Billings' two syntypes of *Heliolites speciosus* and designate them as lectotype (GSC 2240a) and paralectotype (GSC 2240). Both coralla have crenulate tabularia and their coenenchymes possess trabecular rods; the lectotype and paralectotype, respectively, have mean tabularium diameters of 2.45 mm and 2.27 mm, and tabularium areas averaging 32% and 33% of corallite areas (measurements made on external surfaces). These characters are very similar to those for the specimens from the east-central United States (see Table 15; Text-fig. 18); the slightly smaller size of tabularia in GSC 2240 may be attributed to the small size of this corallum (about 27 mm wide, 50 mm high).

Specimens of *P. speciosa* from member 7 at the top of the Ellis Bay Formation on Anticosti Island (Gamachian to possibly lowermost Silurian, Lower Llandovery, lowermost Rhuddanian; Melchin *et al.*, 1991, p. 1861) were described and discussed in detail by Dixon (1974; unit referred to as member 6 therein). They have crenulate tabularia with a mean diameter of 2.6 mm, tabularium areas averaging 37% of corallite areas, spinose septa, and trabecular rods in their coenenchymes. These features are very similar to those for coralla from the east-central United States (see Table 15; Text-fig. 18); the only discernable difference is that the specimens from Anticosti tend to have a lesser degree of thickening of skeletal elements. We agree with Dixon (1974, p. 583) on the synonymization of other Anticosti occurrences of this species. These include the material from Junction Cliff (lower Ellis Bay Formation) illustrated by Lindström (1899) as *P. speciosa* and as *Propora* (*Pinacopora*) *girvanensis* (referred to by Lindström in his text as *Pinacopora grayi*), and other specimens from Junction Cliff listed by Lambe (1899) in his description of *Lyellia americana*. Twenhofel (1928) recognized *Lyellia speciosa* at several levels in the Ellis Bay Formation.

More recently, a corallum of *P. speciosa* from member 7 of the Ellis Bay Formation was illustrated by Bolton (1981a; member 6 interbiohermal therein). This specimen has tabularia with diameters of about 2.5 mm, globose coenenchymal dissepiments, and sparse coenenchymal trabeculae. Bolton's (1981a, pl. 11, figs. 3, 4) *Propora* sp. aff. *P. speciosa* from the Jupiter Formation (Middle–Upper Llandovery, upper Aeronian–Telychian; Barnes, 1988, fig. 2) is distinguished from *P. speciosa* by having irregular or incomplete tabulae that bear small spinules on their upper surfaces, and by lacking septal spines and possessing slightly smaller tabularia.

The specimens described and illustrated here from the east-central United States include the type specimen (UI X-850) of *Calvinia edgewoodensis* (= *Cavella edgewoodensis* according to Stechow, 1922), which is the type species of *Calvinia* (= *Cavella*). Savage's (1913) recognition of *Calvinia* as a new genus was based on the misinterpretation of coenenchymal trabeculae as cylindrical tubules. Of all the material from the east-central United States, the type specimen of *C. edgewoodensis* is the most similar to *P. speciosa* from Anticosti Island (compare Pl. 7, figs. 1–4, with Dixon, 1974, figs. 7b, 8). The corallum of *P. speciosa* from Section-interval 32-1c (Thomson East) is geographically separated from, and is younger than, the four specimens from southern Illinois. Nevertheless, it is similar to them and has numerical characters that are mostly close to the species means (biometric data for USNM 485776: TaD = 2.60 mm, WT = 0.213 mm, LS = 60%; compare with Table 15). Among the other corals from the east-central United States, *P. speciosa* is most similar to *P. savagei* (see *Discussion* under *P. savagei*, p. 58).

Corals from the Grande Coupe beds of the Matapédia Group near Percé, Québec (Upper Ordovician, Ashgill, pre-Hirnantian; Lespérance *et al.*, 1987, fig. 4), were described and illustrated as *P. speciosa* by Bolton (1980; White Head Formation therein). We examined the following specimens: GSC 53531 (Bolton, 1980, pl. 2.5, figs. 1, 6), collected by G. W. Sinclair in 1956, Grande Coupe, Québec; GSC 53532 (Bolton, 1980, pl. 2.5, fig. 3), collected by P. J. Lespérance in 1962, Petite Coupe, Québec. These coralla have crenulate tabularia, spinose septa, and short trabecular rods in their coenenchymes. They differ from those in the Ellis Bay Formation of Anticosti Island by having smaller tabularium diameters of about 1.8–2.2 mm and broad coenenchymal dissepiments, and one (GSC 53532) has tabulae that bear spines on their upper surfaces. For these reasons, they are questionably synonymized with *P. speciosa* here.

A species described by Bondarenko and Minzhin (1981) as *P. speciosa* from the Ashgill Tsagan-Del beds of Mongolia may be conspecific with the North American *P. speciosa*. The Mongolian specimens have tabularia with crenulate outlines and coenenchymes with trabecular rods, but are distinguished by having somewhat smaller tabularium diameters of about 1.3–2.2 mm, by the common occurrence of long, thick, vertically oriented spines on the upper surfaces of tabulae, and by their generally broader coenenchymal dissepiments. Bondarenko and Minzhin (1981, pp. 11, 12) noted that phyletic changes in the Mongolian material include an increase in tabularium diameter, disappearance of the spines on tabulae, and an increase in the length of coenenchymal rods. This pattern is reflected in North America by the differences between the specimens from the Grande Coupe beds and those from the Ellis Bay Formation and the east-central United States.

Proporids that are similar to *P. speciosa* also occur in some parts of Baltoscandia. A specimen from the Porkuni Stage of Estonia (Ashgill, Hirnantian; Kaljo *et al.*, 1988, p. 90), illustrated and briefly described as *Propora magna* by Sokolov (1955, 1962), may be conspecific with *P. speciosa*. It has crenulate tabularia with diameters (outside?) of about 3 mm, but has thinner walls than those of *P. speciosa* and has only small trabecular tubercles, rather than rods, in its coenenchyme.

Lindström (1899, pl. 9, figs. 45, 46, pl. 10, figs. 1–5) illustrated specimens identified as *P. speciosa* from Borenshult, Östergotland (Ostrogothia in Lindström), Sweden (probably of Ordovician age), and from the Slite Beds of Gotland, Sweden (upper Lower Silurian, mid-Wenlock). These are similar to the North American *P. speciosa* in having trabecular rods in their coenenchymes, but we do not consider them to be synonymous. The Östergotland specimens have smaller tabularia with diameters of about 1.5 mm and possess broad coenenchymal dissepiments, and the material from Gotland has smaller and more broadly spaced tabularia with diameters of about 1.7 mm; both appear to lack septal spines.

Propora bacillifera Lindström (1899, p. 97, pl. 10, figs. 8–21) was erected for material from the following locations: Treberga, öland, Sweden (Upper Ordovician; Jaanusson and Mutvei, 1982, p. 9); Dalarna (Dalecarlia in Lindström), Sweden (Ordovician or Silurian); Kõrgessaare, Island of Hiiuama (Hohenholm in Dagö in Lindström), and Piersal, Estonia (both Upper Ordovician, F_I, Nabala, Vormsi, or Pirgu Stage; Twenhofel, 1916, pp. 293, 294; Rõõmusoks, 1960, table 1); Borkholm, Estonia (Ashgill, F_{II}, Porkuni Stage; Twenhofel, 1916, pp. 293, 306; Rõõmusoks, 1960, table 1); Island of Herøy (?; Herö in Lindström), Norway; and Gotland, Sweden (Röda Lagret?; Upper Llandovery, Telychian). Like *P. speciosa*, this species has trabecular rods in its coenenchyme, but its tabularia have diameters of about 3 mm and are more broadly spaced, and it possesses very long and thick septal spines.

Propora bacillifera has also been described and illustrated by Kiaer (1930, p. 68, pl. 5, figs. 2, 3) from the Upper Ordovician of Stord, Norway. Kiaer's material has broadly spaced tabularia with diameters of about 1.8–1.9 mm, and has weakly developed coenenchymal trabeculae and septal spines. It is more similar to *P. speciosa* than to Lindström's *P. bacillifera*, but is probably not conspecific with either species.

Plasmopora conferta (Milne-Edwards and Haime) was identified from the Bønsnes Formation of Ringerike, Norway (Ashgill, Rawtheyan; Owen *et al.*, 1990, p. 37), by Kiaer (1899, pp. 27, 28, pl. 4, figs. 3, 4; Gastropodenkalk, Etage 5a therein). It has spinose septa, coenenchymal trabeculae, and tabularium diameters of about 1.8–3.2 mm, but has much broader coenenchymal dissepiments than those of *P. speciosa.*

Occurrences.—Uppermost Ordovician (Gamachian): Leemon Formation, southern Illinois. Lower Lower Silurian (Lower Llandovery, upper Rhuddanian): upper Mosalem Formation, northwestern Illinois.

Uppermost Ordovician (Gamachian) to lowermost Silurian (?; Lower Llandovery?, lowermost Rhuddanian?): Ellis Bay Formation, Anticosti Island, Québec. Possibly in Upper Ordovician (Ashgill, pre-Hirnantian): Grande Coupe beds, Matapédia Group, near Percé, Québec. Possibly in Upper Ordovician (Ashgill): Tsagan-Del beds, Mongolia.

Lectotype.—Designated here: GSC 2240a (Pl. 6, fig. 5), collected by T. C. Weston in 1865, Ellis Bay Formation, White Cliff, Ellis Bay, Anticosti Island, Québec.

Paralectotype.—Designated here: GSC 2240, collected by T. C. Weston in 1865, Ellis Bay Formation, White Cliff, Ellis Bay, Anticosti Island, Québec.

Other material described above.—Five specimens: UI C-889a, collected by T. E. Savage (labelled "*Plasmopora thebesensis,* Edgewood [Formation], Thebes"), UI C-1438, collected by T. E. Savage (labelled "*Calvinia edgewoodensis,* Edgewood [Formation], near Thebes"), Leemon Formation, Section 31 (Thebes North), Alexander County, Illinois; UI X-850 (type specimen of *C. edgewoodensis*), C-1440, collected by T. E. Savage (labelled "*Calvinia edgewoodensis,* Edgewood [Formation], near Gale"), Leemon Formation, Gale Section, Alexander County, Illinois; USNM 485776, interval 32-1c, Mosalem Formation, Section 32 (Thomson East), Carroll County, Illinois.

Propora species aff. **P. affinis** (Billings, 1865)

Plate 7, figures 9, 10

[*aff.*] *Heliolites affinis* Billings, 1865, pp. 427, 428; 1866, pp. 5, 6.
[*aff.*] *Propora conferta* Milne-Edwards and Haime, 1851. Bolton, 1981a, pl. 9, fig. 1, pl. 11, figs. 1, 2.

Description.—The single corallum of this species is broken. It is of low domical growth form, 58 mm wide and 21 mm high.

In transverse section, tabularia are usually smooth-walled or have slightly wavy walls, but are crenulate where skeletal elements are thickened. Adult tabularia commonly have diameters of 1.0–1.3 mm (Table 15). Tabularia are moderately close-spaced, with tabularium areas averaging 38% of corallite areas (Table 15). In longitudinal section, tabularia are elongate, and straight or gently curved (Pl. 7, fig. 10).

Corallite walls are thin, but exhibit cyclomorphic thickening; thickness varies from 0.025–0.100 mm (Table 15). Septa are absent or are represented by 12 thickened trabecular ridges in cyclomorphically dense parts of the corallum. Septal length is 0–25% of tabularium radius (Table 15). Exothecal projections from septa are rare and small. Tabulae are thin, mostly complete, and flat to strongly concave. Spacing varies cyclomorphically (Pl. 7, fig. 10), averaging about 10 tabulae in 5 mm (Table 15). Tabulae are more densely spaced in bands having thickened skeletal elements; pairs of dense and less dense bands average 4.0 mm in thickness.

In longitudinal section, coenenchyme is composed of globose to moderately broad domed dissepiments. Dissepiments are usually thin and widely spaced; they are more closely spaced in cyclomorphically dense bands. Dissepiments average 13.5 in 5 mm; ratio of corallite tabulae to dissepiments per unit of vertical distance is about 0.8 (Table 15). In transverse section, dissepiments are sparsely distributed.

Corallite increase is coenenchymal. New tabularia were initiated on the upper surfaces of coenenchymal dissepiments.

Discussion.—This corallum has close affinities with members of the group that includes *Propora affinis, Propora conferta,* and *Propora thebesensis.* However, because there is only one poorly preserved specimen, it is not considered possible to make a definite specific assignment. The name *Propora* sp. aff. *P. affinis* is used for this specimen because of its similarity in numerical characters to Billings' syntype of *P. affinis* (GSC 2340, 2340a; see *Discussion* under *P. thebesensis,* p. 53; Text-fig. 15) from the Gun River Formation (Middle Llandovery, lower Aeronian; Barnes, 1988, fig. 2) on Anticosti Island, Québec. It is also closely similar to the specimens illustrated by Bolton (1981a, pl. 9, fig. 1, pl. 11, figs. 1, 2) as *P. conferta* from the Gun River Formation and the Jupiter Formation (Middle–Upper Llandovery, upper Aeronian–Telychian; Barnes, 1988, fig. 2) on Anticosti. Bolton's specimens are distinguished from *Propora* sp. aff. *P. affinis* by their more globose coenenchymal dissepiments, and his corallum from the Gun River Formation may have slightly larger tabularia.

Propora sp. aff. *P. affinis* is distinguished from the older *P. thebesensis,* which also occurs in the east-central United States, by its larger and wider coenenchymal dissepiments, more broadly spaced tabularia (Text-fig. 15), and greatly reduced exothecal projections. A more thorough comparison of members of the *thebesensis* group is given elsewhere (see *Discussion* under *P. thebesensis,* pp. 53–55).

Occurrence.—Lower Lower Silurian (Lower Llandovery, upper Rhuddanian, or possibly Middle Llandovery, lowermost Aeronian): Elwood Formation, northeastern Illinois.

Material described above.—One specimen: USNM 485777, interval 29-4, Elwood Formation, Section 29 (Sears Pit), De Kalb County, Illinois.

Propora species A

Plate 8, figures 1, 2

Description.—The single corallum of this species is broken. It is probably of low domical growth form, more than 75 mm wide and more than 33 mm high.

In transverse section, tabularia have irregular crenulate outlines (Pl. 8, fig. 1); adult diameters are commonly 2–3 mm (Table 15). Tabularia are wide-spaced, with tabularium areas averaging 20% of corallite areas (Table 15). In longitudinal section, tabularia are almost straight or of irregular shape (Pl. 8, fig. 2).

Corallite walls are moderately thick, ranging from 0.125–0.175 mm (Table 15). Walls are composed of trabecular septal bases, with additional trabeculae irregularly distributed between them. Walls are complete where thickened, but are sometimes incomplete where unthickened; incomplete walls are composed of the lateral edges of coenenchymal dissepiments (Pl. 8, fig. 2). Septa have variably developed trabecular bases with abundant, moderately thick, straight or curved spinose extensions. Septal spines are more abundant in zones of septal thickening; they may project through tabulae and become interspersed with tabular spines (Pl. 8, fig. 2). Length of septa is about three-quarters of tabularium radius (Table 15). Exothecal projections from septa are present in some cases.

Tabulae are closely but variably spaced, averaging about 13 in 5 mm (Table 15). They are flat, convex, concave, or wavy, and incomplete or dissepimentate in some zones (Pl. 8, fig. 2). Abundant short, thick trabecular spines project from the upper surfaces of tabulae (Pl. 8, fig. 2).

In longitudinal section, coenenchyme consists of variable, low-domed to globose dissepiments; in some cases these are very broad. They commonly bear short, thick spines (diameter 0.05–0.15 mm) on their upper surfaces. Dissepiments are moderately closely spaced, about 11 in 5 mm (Table 15). They are more broadly spaced than corallite tabulae; ratio of tabulae to dissepiments per unit of vertical distance is 1.25 (Table 15). Although spacing of both tabulae and dissepiments is variable, cyclicity is poorly developed. In transverse section, coenenchyme appears as irregular curved plates interspersed with the small trabecular spines (Pl. 8, fig. 1).

Discussion.—This corallum is different from most members of *Propora* in having spines developed on its septa, tabulae, and coenenchymal dissepiments. It is clearly similar to the somewhat younger *Propora glabra* Owen (1844). The latter species was described and illustrated by Milne-Edwards and Haime (1851, pp. 226, 227, pl. 12, figs. 2, 2a–c) from the "Magnesian Limestone" of Iowa (Hopkinton Dolomite?: lower Lower Silurian, Middle–Upper Llandovery, Aeronian–Telychian; Witzke, 1992, fig. 18), and by Stumm (1965, pp. 57, 58, pl. 56, figs. 7–9) from the Manistique Dolomite of Michigan and Ontario (Upper Llandovery; Winder and Sanford, 1972, fig. 2), Hopkinton Dolomite of Iowa, and Louisville Limestone of Indiana and Kentucky (upper Lower Silurian, Upper Wenlock; Berry and Boucot, 1970, p. 180). *Propora glabra* has crenulate tabularia with diameters of about 2.0–2.5 mm, incomplete tabulae, and spines on both tabulae and coenenchymal dissepiments, but it seems to have longer and thicker septa than does the corallum described above. The *P. glabra* illustrated by Bolton (1981a, pl. 13, fig. 7), from the Chicotte Formation of Anticosti Island, Québec (Upper Llandovery, Telychian; Barnes, 1988, fig. 2), is quite different, having more widely spaced tabularia with diameters less than 2 mm and tabulae that appear to lack spines.

This corallum is identified as *Propora* sp. A. It is not assigned to a new species because only one incomplete specimen is known.

Occurrence.—Lower Lower Silurian (Lower? Llandovery, upper Rhuddanian?): Sexton Creek Limestone, southern Illinois.

Material described above.—One specimen: UI C-1403, collected by T. E. Savage (labelled "*Lyellia americana,* Sexton Creek [Limestone], Thebes"), Sexton Creek Limestone, near Thebes, Alexander County, Illinois.

Family **PLASMOPORIDAE** Sardeson, 1896

Genus **PLASMOPORA**

Milne-Edwards and Haime, 1849

Plasmopora Milne-Edwards and Haime, 1849, p. 262.
Laminoplasma Bondarenko, 1963, p. 49.
Eolaminoplasma Bondarenko, 1963, p. 50.

Type species.—By monotypy: *Porites petalliformis* Lonsdale (1839, p. 687, pl. 16, figs. 4, 4a); Wenlock Shale (upper Lower Silurian, Wenlock), Walsall, U.K.

Diagnosis.—"Plasmoporidae with corallites of smooth or crenulate outline; each corallite surrounded by a complete aureole of tubules; coenenchyme between aureoles of irregular tubules in transverse section; dissepimentate in vertical section with spines, rods, or vertical plates irregularly outlining tubules; tabulae mostly complete" (Young and Noble, 1990b, p. 194).

Table 16.—Biometric data for one corallum of *Plasmopora* sp. cf. *P. logani* (UI C-865b) from the east-central United States. *TaD* = tabularium diameter, *TaA* = tabularium area, *CoA* = corallite area, *TuD* = tubule diameter, *WT* = wall thickness, *LS* = length of septa, *Ta5* = number of tabulae in 5 mm, *Di5* = number of coenenchymal dissepiments in 5 mm; c.v. = coefficient of variation.

	parameters									
data	*TaD*	*TaA*	*CoA*	*TaA:CoA*	*TuD*	*WT*	*LS*	*Ta5*	*Di5*	*Ta5:Di5*
mean	1.32 mm	1.37 mm^2	4.12 mm^2	0.33	0.38 mm	0.056 mm	0	8.8	11.4	0.77
minimum	1.15 mm	—	—	—	0.20 mm	0.050 mm	—	6	9	—
maximum	1.45 mm	—	—	—	0.65 mm	0.075 mm	—	11	15	—
intracolony c.v.	6.7	—	—	—	26.3	19.6	—	20.5	20.2	—

Remarks.—The concept of *Plasmopora* given by Young and Noble (1990b, pp. 194, 195) is followed here. The specimen described below as *Plasmopora* sp. cf. *P. logani* is the oldest known North American *Plasmopora* and one of the oldest worldwide. It is similar in characters such as tabularium diameter and form of septa to *Propora thebesensis,* which also occurs in the east-central United States. This similarity suggests that *Plasmopora* sp. cf. *P. logani* descended from a proporid belonging to the *thebesensis* group. *Plasmopora* as presently defined is an extremely variable genus, and other species groups assigned to it appear to have evolved later from different ancestral taxa.

Plasmopora species
cf. **P. logani** Young and Noble, 1990b
Plate 8, figures 3, 4

[*cf.*] *Plasmopora follis* Milne-Edwards and Haime, 1851. Lambe, 1899, pp. 82, 83, pl. 2, figs. 8, 8a; Northrop, 1939, p. 148; Noble and Young, 1984, pp. 874, 875, figs. 5c, 5d, 8.

[*cf.*] *Pseudoplasmopora follis* (Milne-Edwards and Haime, 1851). Bolton, 1981b, pl. 3, figs. 5, 6, pl. 4, figs. 8, 9.

[*cf.*] *Plasmopora logani* Young and Noble, 1990b, p. 195, figs. 6.6–6.11, 7.1–7.3.

Description.—The single corallum is high bulbous and flat-based. It is 26 mm wide and 19 mm high.

In transverse section, tabularia are circular or subcircular, smooth-walled, rarely irregular in outline (Pl. 8, fig. 4). Adult tabularia have diameters of 1.15–1.45 mm (Table 16). Tabularium spacing is moderate; tabularium areas average 33% of corallite areas (Table 16). In longitudinal section, tabularia are straight or gently curved.

Corallite walls are regular and moderately thick; averaging about 0.06 mm, but are more thickened in places (Table 16). Thickening of walls may extend outward into walls of adjacent coenenchymal tubules. Septa are usually absent; weak septal ridges occur rarely (Pl. 8, fig. 4). Tabulae are complete, horizontal or slightly concave, and wide-spaced, averaging about nine in 5 mm (Table 16). Cyclicity of tabular spacing is poorly developed.

In longitudinal section, high-domed, narrow, thin coenenchymal dissepiments are vertically aligned but do not usually form definite tubules (Pl. 8, fig. 3); they are occasionally arranged into clearly defined tubules in some small areas. About 11 dissepiments in 5 mm; ratio of corallite tabulae to dissepiments per unit of vertical distance averages 0.77 (Table 16). In transverse section, coenenchyme is composed of polygonal tubules of variable size; average diameter about 0.4 mm (Table 16). Tubule walls are generally thin. Each tabularium is usually surrounded by an aureole of 12 tubules. One or two tubules, rarely three or four, occur between pairs of adjacent tabularia (Pl. 8, fig. 4).

Corallite increase is coenenchymal. The base of each new tabularium was initiated across the tops of several laterally equivalent coenenchymal dissepiments.

Discussion.—This corallum is remarkably similar to the younger *Plasmopora logani,* which occurs in the lower Lower Silurian (Upper Llandovery, Telychian) to upper Lower Silurian (Lower Wenlock) Anse à Pierre-Loiselle, Limestone Point, and La Vieille formations of northern New Brunswick and the southern Gaspé Peninsula of Québec. *Plasmopora logani* also lacks septa or has weak septal ridges, possesses a coenenchyme similar in appearance to that of our specimen, and has numerical characters that are virtually identical (biometric data for *P. logani*, based on Young and Noble, 1990b, table 4: mean corallum tabularium diameters of 0.96–1.40 mm, mean TuD = 0.30 mm, mean WT = 0.06 mm, TaA:CoA = 0.32; compare with Table 16). Our specimen is identified as *Plasmopora* sp. cf. *P. logani* because of its significantly greater age, and because it is the only known specimen. It is considered to belong to the same lineage as *P. logani.*

Prior to the work of Young and Noble (1990b), *P. logani* from northern New Brunswick and the Gaspé Peninsula had been identified as *Plasmopora follis* or as *Pseudoplasmopora follis.* Young and Noble (1990b, p. 195) discussed the characters that distinguish *P. logani* from *P. follis* and other species.

Plasmopora sp. cf. *P. logani* was listed as *Plasmopora* sp. A by Elias and Young (1992, fig. 2, tables 1, 2).

Occurrence.—Uppermost Ordovician (Gamachian) to lowermost Silurian (?; Lower Llandovery?, lower

Rhuddanian?): Cyrene Formation, northeastern Missouri.

Material described above.—One specimen: UI C-865b, collected by T. E. Savage (labelled "*Lyellia thebesensis*, Edgewood [Formation], Edgewood"), Cyrene Formation, near Edgewood, Pike County, Missouri.

Family **COCCOSERIDIDAE** Kiaer, 1899

Genus **ACIDOLITES**
Lang, Smith, and Thomas, 1940
pro **Acantholithus** Lindström, 1899
(*non* Stimpson, 1858)

Acidolites Lang *et al.*, 1940, p. 13.

Type species.—By original designation: *Acantholithus lateseptatus* Lindström (1899, p. 113, pl. 11, figs. 23–30); probably Ordovician (found in a Pleistocene moraine), Kopparsvik, Gotland, Sweden.

Diagnosis.—"Corallites with partly dilated septa and narrow interseptal spaces crossed by tabulae or with fully dilated septa, no interspaces and no tabulae. Septal trabeculae abut or curve upward into a solid columella of vertical trabeculae. Coenenchyme wide or narrow, with trabeculae arranged to form vertical tubules. Coenenchymal trabeculae variously dilated, resulting in continuous or discontinuous openings, crossed by transverse diaphragms. Trabecular structure evident on surface of corallum as rounded or acute tubercles defining the outlines of coenenchymal tubules and corallites, and in the calices arranged along the edges of septa and clustered on an axial boss terminating the columella." (From Dixon, 1986, p. 29.)

Remarks.—Dixon's (1986, pp. 29, 30) paper on *Acidolites* from eastern North America provides a thorough discussion. His concept of this genus is followed here.

Acidolites species A
Plate 8, figures 5–7

Description.—The single corallum has a high domical growth form. It is extremely small, measuring 8.0 mm wide and 6.6 mm high (Pl. 8, fig. 5).

In transverse section, tabularia are strongly crenulate and very small, with diameters of about 0.65–0.70 mm. Tabularia appear to be wide-spaced. Each tabularium is defined by 12 distinct, thick, contiguous septal trabeculae (Pl. 8, fig. 6); long axis (transverse) of each trabecula is about 50–75% of tabularium radius. Septal trabeculae form the corallite wall, and in some places have exothecal extensions. Septa have upturned spinose tips that form a pseudocolumella in the center of each tabularium; diameters of tips are about 0.050–0.075 mm. In longitudinal section, each tabularium is straight or slightly curved, and is bounded by a thick tabularium on either side. Tabulae are moderately thick, variably and widely spaced (Pl. 8, fig. 7).

In transverse section, the coenenchyme consists of thick irregular trabeculae with diameters of 0.075–0.175 mm; spaces between these trabeculae are present in some places (Pl. 8, fig. 6). In longitudinal section, coenenchymal trabeculae are regular, straight or slightly curved, with flattened bases (Pl. 8, fig. 7).

Discussion.—This corallum has septal and coenenchymal trabeculae that are greatly dilated, and is near one extreme of variation for these characters in *Acidolites*. It is most similar to *Acidolites compactus* Dixon (1986, pp. 39, 40, 42, figs. 7.1–7.7, 10), from member 7 at the top of the Ellis Bay Formation (uppermost Ordovician, Gamachian, to possibly lowermost Silurian, Lower Llandovery, lowermost Rhuddanian) and from the lower Becscie Formation (lower Rhuddanian; Melchin *et al.*, 1991, p. 1861) on Anticosti Island, Québec. The latter species was illustrated by Bolton (1981a, pl. 4, figs. 1, 2) as *Acidolites* sp. Type 2. Like our corallum, *A. compactus* has greatly dilated coenenchymal and septal trabeculae, but its septa are so highly dilated that tabulae are not seen, and its tabularium diameter of 1.1–1.4 mm is much larger.

This corallum is identified as *Acidolites* sp. A. It is not assigned to a new species because only one extremely small corallum is known.

Occurrence.—Uppermost Ordovician (Gamachian): Leemon Formation, southern Illinois.

Material described above.—One specimen: UI C-889b, collected by T. E. Savage (in matrix of specimen labelled "Edgewood [Formation], Thebes"), Leemon Formation, Section 31 (Thebes North), Alexander County, Illinois.

Genus **PROTARAEA**
Milne-Edwards and Haime, 1851

Protaraea Milne-Edwards and Haime, 1851, pp. 146, 208.
[?] *Coccoseris* Eichwald, 1855–1860, p. 2.

Type species.—By subsequent designation (Miller, 1889, p. 201): *Porites vetustus* Hall (1847, p. 71); Trenton Limestone (upper Middle Ordovician), New York, U.S.A.

Diagnosis.—Corallum of thin sheets, commonly encrusting. Corallites close to apparently widely spaced; coenenchyme absent to apparently wide, when present of closely contiguous thick trabeculae perpendicular to surface. Twelve septa of contiguous trabeculae directed steeply upward and filling the lumen. Tabulae absent.

Remarks.—The generic concept we follow is similar to that of Hill (1981, p. F622), except that the material

Table 17.—Biometric data for one corallum of *Protaraea* sp. A (USNM 485778) from the east-central United States. *TaD* = tabularium diameter, *TaA* = tabularium area, *TuD* = tubule diameter, *TC* = thickness of cycles; c.v. = coefficient of variation.

	parameters			
data	*TaD*	*TaA*	*TuD*	*TC*
mean	0.89 mm	0.62 mm^2	0.182 mm	1.92 mm
minimum	0.75 mm	—	0.100 mm	0.60 mm
maximum	1.10 mm	—	0.275 mm	4.05 mm
intracolony c.v.	14.7	—	20.9	—

described here as *Protaraea* sp. A has more broadly spaced tabularia than would be permitted by Hill's definition. In this feature, *Protaraea* sp. A is transitional between *Protaraea* and *Coccoseris;* Sokolov's (1955, p. 466) suggestion that *Coccoseris* is a junior synonym of *Protaraea* may be correct. Neither genus has been analyzed in any detail in the modern literature, however, and the type material requires restudy.

Protaraea species A
Plate 8, figures 8–12

Description.—Laminar corallum growth forms predominate; two of the three coralla form sheets about 0.50–2.25 mm thick, and encrust calcareous algae, brachiopods, and *Halysites alexandricus* (Pl. 8, fig. 12). The one taller corallum (Pl. 8, fig. 8) consists of a vertical stack of horizontal layers with an average thickness of 1.92 mm (Table 17). Layers are separated by sediment inclusions that represent levels where polyps had died prior to colony regeneration.

Contiguous trabeculae fill all tabular and coenenchymal space. Tabularia are crenulate in outline, with adult diameters of 0.75–1.10 mm (Table 17); they are difficult to recognize in transverse sections (Pl. 8, figs. 10, 11). Tabularia appear to be widely spaced; tabularium areas are about 10–20% of corallite areas, but spacing cannot be determined with certainty because of difficulty in discriminating tabularia from coenenchyme. Tabularia are filled with dense polygonal trabeculae; 12 large, regular septal trabeculae with diameters of about 0.225–0.300 mm occur inside each tabularium boundary, with about six smaller trabeculae having diameters of about 0.100–0.275 mm in the center of each tabularium (Pl. 8, fig. 11). In some tabularia, trabeculae are separated from one another by thin, dark lines. Tabularia cannot be distinguished in longitudinal sections.

Corallites lack distinct walls other than the septal trabeculae. In some cases, however, a dark line separates trabeculae in a tabularium from those in the adjacent coenenchyme (Pl. 8, fig. 11). Tabulae are absent.

In transverse section, coenenchyme is composed of polygonal trabeculae with diameters of about 0.100–0.275 mm (Table 17; Pl. 8, figs. 10, 11). Thin, dark lines separate trabeculae in some places (Pl. 8, fig. 11). In longitudinal section, trabeculae are straight or gently curved, with flat or gently rounded bases (Pl. 8, figs. 8, 9) and tips that are pointed and triangulate, or somewhat rounded (Pl. 8, fig. 9).

Discussion.—These coralla are referred to *Protaraea* because their coenenchymes are composed of contiguous trabeculae, and the tabularia are completely filled with trabecular septa and lack tabulae. They are not very similar to any of the species of *Protaraea* that are well documented in the literature, however, because their tabularia are both smaller and much farther apart. This latter character may suggest that these coralla could be better placed in *Coccoseris,* but they have upward-directed septal trabeculae rather than the axially directed septal trabeculae that are apparently typical of that taxon (see *Remarks* under *Protaraea,* pp. 65, 66). These specimens are identified as *Protaraea* sp. A; they are not assigned to a new species because they are few in number and because the type of preservation does not permit complete description and analysis of characters.

Among other species, *Protaraea guijangensis* Lin (1965, pp. 78, 85, pl. 4, fig. 2), from the Upper Ordovician of Guizhou Province, China, may be the most similar to *Protaraea* sp. A. *Protaraea guijangensis* has similar spacing of tabularia, but has somewhat larger tabularia with diameters of about 1.2–1.5 mm. Unfortunately, Lin's illustration shows only a poorly preserved external surface, so detailed comparisons are not possible.

Occurrence.—Uppermost Ordovician (Gamachian): lower Keel Formation, south-central Oklahoma.

Material described above.—Three specimens: USNM 485778, site 23i, USNM 485779c, site 23iii, USNM 485780c, site 23iv, interval 23-2 (*Brevilamnulella* beds), Keel Formation, Section 23 (Lawrence Quarry), Pontotoc County, Oklahoma.

Order **HALYSITIDA** Sokolov, 1947

Diagnosis.—Tabulata with thick-walled corallites arranged in uniserial ranks that join to surround lacunae. Septa consist of up to 12 rows of spines and/or longitudinal ridges, rarely more; may be absent. Tabulae usually complete. Adjacent corallites in ranks may or may not be separated by tubules having horizontal or convex tabulae. Corallite increase lateral or interstitial.

Discussion.—Hill (1981, pp. F602, F603) considered halysitids to be a suborder within the Heliolitida on the basis of shared characters including the presence of coenenchyme between corallites and septa typically numbering 12. The former character is almost certainly not homologous, since halysitids having tubules between their corallites are unknown before the upper Caradoc in the Ordovician, apparently having evolved from the non-tubular forms that had first appeared during the Blackriveran (Middle Ordovician). The shared septal number may indicate that halysitids and heliolitids had a common origin, but inclusion within a single order suggests a degree of similarity that is absent between these discrete, internally consistent groups. For these reasons, we follow Scrutton (1985, pp. 34, 36) in recognizing the Halysitida as an order distinct from the Heliolitida.

Family **HALYSITIDAE**
Milne-Edwards and Haime, 1849

Genus **HALYSITES** Fischer von Waldheim, 1828

Alyssites Fischer von Waldheim, 1813, p. 387.
Halysites Fischer von Waldheim, 1828, p. 15.
Schedohalysites Hamada, 1957, p. 401.
Acanthohalysites Hamada, 1957, p. 404.

Type species.—By monotypy: *Tubipora catenularia* Linnaeus (1767, p. 1270); Silurian, Gotland, Sweden.

Diagnosis.—Halysitidae with circular, elliptical, or subquadrate corallites arranged in uniserial ranks. Septa consist of rows of spines and/or longitudinal ridges; may be absent. All or most corallite tabulae are complete. Tubules occur between some or all corallites; tubule tabulae complete.

Discussion.—Our concept of *Halysites* is similar to that put forward by Laub (1979, pp. 271–274). His inclusion of *Schedohalysites* and *Acanthohalysites* as junior synonyms is followed here.

There is one major problem associated with the recognition of *Halysites*. The development of tubules in halysitids is a variable character, and it is not easy to draw a boundary between *Halysites* and *Catenipora*, which completely lacks tubules. Hamada (1957) dealt with this problem by erecting *Schedohalysites* to include those halysitids that possess tubules between some corallites but lack them between others. As Laub (1979, p. 274) noted, however, tubules are not universally present in many species of *Halysites;* their absence from parts of a corallum may be due to developmental stage or to poor preservation. Laub suggested that specimens should be included in *Halysites* if they possess any tubules at all.

A further complication is that certain specimens, including those described below as *Halysites* sp. cf. *H. alexandricus* and *Halysites*? sp. A, possess structures that appear to be tubules that were filled with skeletal material during subsequent growth. Although some species with completely infilled tubules probably evolved from others with open tubules, they would be placed in *Catenipora* according to presently accepted definitions of these genera. Flower (1961, p. 47) considered corals with such features to be "advanced" members of *Catenipora*. Examples in the literature suggest that this problem may involve a number of species (*e.g., Catenipora crassa* Stasinska; see Stasinska, 1967, pp. 43, 44, pl. 7, fig. 1). A classification that would take this into account would necessarily be based on a thorough re-examination of halysitid structure, microstructure, and phylogeny; this is beyond the scope of the present study.

Hill (1981, p. F627) assigned *Halysites* to the subfamily Halysitinae Milne-Edwards and Haime and *Catenipora* to the subfamily Cateniporinae Hamada. We do not recognize those subfamilies because of problems associated with the distinction of *Catenipora* from *Halysites*, as discussed above.

Halysites alexandricus, new species
Plate 9, figures 1–11; Plate 10, figures 1–10;
Plate 11, figures 1–6

Derivation of name.—The species name is derived from Alexander County, Illinois, where the type locality, Section 31 (Thebes North), is situated.

Diagnosis.—*Halysites* with ranks of variable length, commonly one to six corallites between rank junctions. Tabularium dimensions usually with length 1.0–1.8 mm, width 0.7–1.4 mm. Septal spines present, variably developed. Tabulae wide-spaced, usually complete. Tubules small, length 0.1–0.3 mm, width 0.1—0.5 mm. Tubules do not occur between every pair of adjacent corallites, are rarely seen in longitudinal sections. Walls between corallites and tubules are thick.

Description of coralla.—Coralla are of low and high bulbous and low domical growth forms (Table 14). Three measured specimens are 33–83 mm wide and 18–43 mm high.

Corallites are arranged in ranks of extremely variable length; commonly one to six corallites between rank junctions (Pl. 9, fig. 4, Pl. 10, fig. 9), occasionally up to 47 corallites without a junction. Density of corallite spacing appears to be related to rank length, with closely spaced corallites occurring in coralla having short ranks. Ranks are broadly curved, and moderately to strongly constricted at intercorallites; they define wide lacunae having subparallel sides. Lacunae are straight, sinuous, or rarely subpolygonal (Pl. 9, fig. 4, Pl. 10, figs. 2, 7, 9, Pl. 11, fig. 3). Rank junctions occur most commonly at lateral corallite walls, rarely at tubules.

In transverse section, corallites are subovate, subelliptical, or subquadrate (Pl. 9, figs. 2, 9, Pl. 10, figs. 2, 6, 7, Pl. 11, figs. 1, 3, 5); they often have flat ends at intercorallites. Tabularia commonly have length 1.0–1.8 mm and width 0.7–1.4 mm (Table 18). Where a rank junction occurs along a lateral corallite wall, the junction corallite is often distorted in the direction of the side rank (Pl. 10, figs. 6, 9, Pl. 11, fig. 3). In longitudinal section, corallites are straight, curved, or somewhat geniculate (Pl. 9, fig. 8, Pl. 10, figs. 3, 5, Pl. 11, figs. 2, 6).

Three distinct "megacorallites" (see Dixon, 1976) are recognized in a transverse section of one specimen (USNM 485781); they are unusually large, with tabularium dimensions up to 3.6 mm by 2.5 mm (Pl. 10, fig. 2). One of the "megacorallites" is subquadrate, with angulate lateral corallite walls, and occurs within a rank that is otherwise normal. The second and third "megacorallites" occur at successive meanders where one rank approaches close to other ranks. The second "megacorallite" is subtriangular, with an angulate lateral wall facing the nearby rank; the opposite lateral wall is normal. The third "megacorallite" is subquadrate, with one of its two angulate lateral walls abutting against the other rank (Pl. 10, fig. 2). In a different specimen (USNM 485800a), several irregularly shaped corallites occur along one side of the corallum (Pl. 10, fig. 9).

Corallite walls are thick or very thick, commonly 0.2–0.4 mm (Table 18). Walls between tabularia and tubules are moderately thick; where tubules are absent, walls between adjacent tabularia are thick. Septa are thorn-like spines that may have broadly thickened bases (Pl. 9, figs. 3, 10). They are rare to abundant, numbering from 0 to 14 in a transverse section of a corallite. Septal length is variable, averaging 22% of tabularium radius but reaching 52% of radius (Table 18). In longitudinal section, septal spines are arranged in rows; they are directed slightly upward, and are straight or curved (Pl. 9, figs. 6, 7).

Tabulae are thin, flat, slightly concave or convex, or irregular. They are usually complete (Pl. 10, figs. 3, 5, 8, 10), rarely incomplete (Pl. 9, fig. 5), and in some cases have crook-shaped, concave depressions. Tabular spacing is broad, variable or regular, averaging about 6 tabulae in 5 mm (Table 18); in some cases spacing shows well-defined cyclomorphic patterns. Tabulae rarely show significant thickening.

In transverse section, tubules are small, commonly with length 0.1–0.3 mm and width 0.1–0.5 mm (Table 18). They are of variable shape: subcircular (Pl. 9, fig. 11, Pl. 10, fig. 1); width greater than length, slit-like or subrectangular (Pl. 9, fig. 1, Pl. 10, fig. 2); rarely length greater than width; in some cases discontinuous and divided into two or three compartments. Tubules are usually aseptate (Pl. 9, fig. 11), but rarely possess short, apparently spinose septa. Lateral walls of tubules are usually thick. Tubules do not occur between every pair of adjacent corallites, and are commonly infilled with skeletal material. Tubules occurring at rank junctions are much larger than usual and are irregular in shape (Pl. 9, fig. 9). Tubules are rarely seen in longitudinal sections. Tubule tabulae are wide-spaced, numbering about 7 in 5 mm, and are flat or slightly concave (Pl. 9, figs. 5, 6, Pl. 11, fig. 4).

Astogeny and corallite increase.—Most observations are based on one serial-sectioned corallum (USNM 485779a). Other specimens are used for comparison.

The protocorallite is not known. In transverse section, corallites occurring in the initial part of a corallum are subelliptical, small, length 0.85–0.95 mm and width 0.5 mm, thick-walled, and possess some short to moderately long septa. Corallites form short ranks that follow the contours of the substrate; ranks are of two to three corallites, initially spreading without joining to surround lacunae. In longitudinal section, bases of corallites occurring in the initial part of a corallum may be flattened, or may conform to the shape of a hard substrate such as a stromatoporoid (Pl. 9, fig. 8). The initial growth of corallites was nearly vertical (Pl. 9, fig. 8) to reptant.

Above the basal part of a corallum, corallites are larger and their septa are commonly longer, though septal development varies vertically throughout the height of a corallite. The form of ranks changes, becoming longer, more sinuous, and subparallel; ranks join to surround elongate lacunae. In longitudinal section, corallites are long, often extending from the base to the upper growth surface (Pl. 9, fig. 8); corallite mortality within a corallum is rarely observed.

Corallite increase may be interstitial (between adult corallites in a rank) or lateral (at the end or side of a rank). Interstitial increase occurred through the expansion of an existing tubule. New corallites in such positions are subquadrate to subelliptical, with proportions similar to those of adult corallites (Pl. 9, figs. 2, 9, Pl. 10, fig. 7). In some cases, new tabularia have quite strongly developed septa (Pl. 9, fig. 9). New tubules were added on either side of each new corallite higher in the colony. In one corallum (UI X-8723), some corallite lumina are connected through gaps in the intercorallite wall, with continuous tabulae occurring between tabularia in some places.

Lateral increase occurred at the ends of ranks or on the lateral margins of adult corallites within ranks. In most cases, no tubule is present between the basal part of the new corallite and the parent corallite; the tubule was added during subsequent growth. In one corallum (USNM 485809; see Pl. 11, fig. 4), however, a new corallite was initiated after the intervening tubule was already in place.

Table 18.—Biometric data for halysitids from the east-central United States. *TaD* = tabularium dimensions (*L* = length, *W* = width), *TaA* = tabularium area, *TuD* = tubule dimensions (*L* = length, *W* = width), *WT* = wall thickness, *LS* = length of septa, *Ta5* = number of tabulae in 5 mm; s.d. = standard deviation, c.v. = coefficient of variation.

species	*parameters*							
data	*TaD (L)*	*TaD (W)*	*TaA*	*TuD (L)*	*TuD (W)*	*WT*	*LS*	*Ta5*
Halysites alexandricus								
mean	1.47 mm	1.03 mm	1.20 mm^2	0.23 mm	0.31 mm	0.305 mm	22%	6.2
range of colony means	1.22–1.68 mm	0.77–1.28 mm	0.74–1.69 mm^2	0.12–0.36 mm	0.19–0.54 mm	0.196–0.394 mm	5–52%	5.1–8.3
s.d. of colony means	0.13 mm	0.15 mm	0.26 mm^2	0.08 mm	0.14 mm	0.052 mm	14%	1.0
c.v. of colony means	8.7	14.1	21.6	36.5	44.8	17.1	63.1	15.5
minimum	0.35 mm	0.60 mm	—	0.05 mm	0.10 mm	0.150 mm	—	3
maximum	2.20 mm	1.70 mm	—	0.45 mm	0.70 mm	0.500 mm	—	10
mean intracolony c.v.	14.1	13.7	—	43.0	31.1	12.4	—	16.5
no. of coralla studied	20	20	20	7	7	16	11	15
Halysites sp. cf. *H. alexandricus*								
mean	1.38 mm	0.85 mm	0.92 mm^2	0.14 mm	0.12 mm	0.186 mm	48%	11.9
minimum	1.10 mm	0.65 mm	—	0.10 mm	0.10 mm	0.150 mm	—	10
maximum	1.55 mm	1.35 mm	—	0.20 mm	0.20 mm	0.275 mm	—	14
intracolony c.v.	8.7	16.5	—	26.9	34.9	21.5	—	14.3
no. of coralla studied	1	1	1	1	1	1	1	1
Halysites? sp. A								
mean	2.49 mm	1.44 mm	2.82 mm^2	—	—	0.210 mm	28%	11.3
minimum	2.00 mm	1.25 mm	—	—	—	0.150 mm	—	10
maximum	2.85 mm	1.70 mm	—	—	—	0.250 mm	—	12
intracolony c.v.	9.6	9.7	—	—	—	15.2	—	10.6
no. of coralla studied	1	1	1	—	—	1	1	1
Catenipora lawrencica								
mean	0.57 mm	0.36 mm	0.16 mm^2	—	—	0.164 mm	19%	13.2
range of colony means	0.49–0.70 mm	0.29–0.47 mm	0.11–0.26 mm^2	—	—	0.150–0.175 mm	—	—
s.d. of colony means	0.08 mm	0.08 mm	0.06 mm^2	—	—	0.013 mm	—	—
c.v. of colony means	14.2	21.4	37.7	—	—	22.0	—	—
minimum	0.35 mm	0.20 mm	—	—	—	0.100 mm	—	11
maximum	0.85 mm	0.60 mm	—	—	—	0.225 mm	—	16
mean intracolony c.v.	11.8	13.0	—	—	—	22.0	—	14.4
no. of coralla studied	6	6	6	—	—	4	1	1

Microstructure.—Corallite walls are fibrous, consisting of an inner and an outer layer. Relative thicknesses of the two layers are variable, but they are usually approximately equal. The outer layer of the wall covers the outer margin of each rank along the edges of both corallites and tubules (Pl. 9, figs. 2, 9, 11). It is usually dark in color, and has growth lamellae oriented parallel to the wall in transverse section. In longitudinal section, lamellae are directed obliquely outward with height in the corallum at an angle of about 20° from vertical, presumably parallel with the former position of polyp tissue (Pl. 9, figs. 6, 7). In longitudinal sections of some corallites, the lamellae of the outer wall interdigitate with the inner wall material.

The inner layer of the wall is paler than the outer one. In transverse sections of corallites, fibers in this layer are seen in oblique cross section, and appear approximately parallel to the wall (Pl. 9, figs. 3, 10). In longitudinal sections they are elongate, directed upward adaxially at angles from the horizontal of 0–60°, usually 30–45° (Pl. 9, figs. 6, 7). In the intercorallite area, the inner wall continues as a pale surface layer (Pl. 9, figs. 2, 11); a darker area occurs farther inside the intercorallite, but other pale areas are seen around some tubules (Pl. 9, fig. 11). In many specimens the darker intercorallite wall material includes poorly defined fibrous bundles (Pl. 9, figs. 2, 11) that probably represent the "balken" of Fischer-Benzon (1871, pp. 14, 15). Septal spines are thorn-like, apparently fibrous, and are embedded in the inner corallite wall; they are darker than that wall, usually about the same color as the outer wall (Pl. 9, figs. 2, 6, 7, 10). The inner wall is often deflected into the lumen around a septal spine (Pl. 9, figs. 10, 11).

Both wall layers are commonly affected by diagenetic alteration. With low-level alteration, the inner wall may take on a lamellar appearance with lamellae parallel to those of the outer wall. With a higher degree of diagenesis, both walls may be composed of continuous fibers oriented perpendicular to the wall in transverse section, or may even take on a pseudotrabecular appearance.

Corallite tabulae are dark-colored and are embedded in the axial edges of the inner corallite wall (Pl. 9, figs. 6, 7). Tabular structure is indistinct, but appears to consist of fibers oriented perpendicular to the plane of each tabula. Tubule tabulae are also dark in color, and abut the edges of the intercorallite walls (Pl. 9, fig. 6); their structure cannot be distinguished.

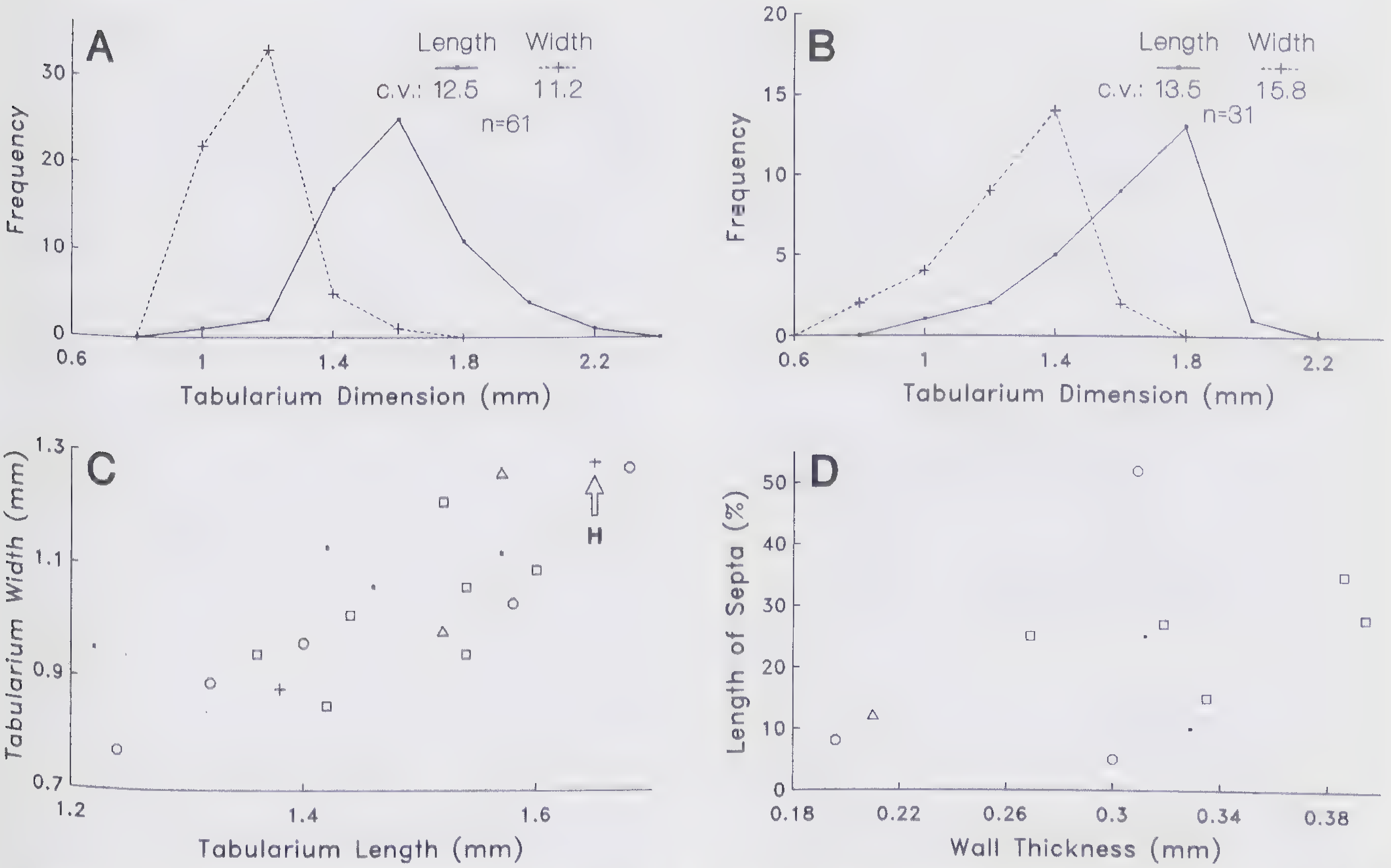
Intraspecific variation.—This species is variable in many characters, such as septal development and the length and arrangement of ranks. The fragmentary nature of many specimens limits the analysis of much of this variation, however, and the data are insufficient for determination of interlocality differences in most characters.

Frequency distributions for tabularium dimensions in two coralla are approximately normal, with length and width having similar curves in each example (Text-fig. 19A, B). Size ranges for both dimensions tend to be relatively broad. The holotype (USNM 485781) has three "megacorallites" that are irregular in outline and about twice the dimensions of normal corallites (*e.g.*, Pl. 10, fig. 2); these are not included in the frequency distribution for the specimen.

A graph of tabularium mean length and width (Text-fig. 19C) indicates that the ratio of these dimensions remains constant at about 1.3–1.4, regardless of the mean corallite size for a corallum. At each locality for which a large number of specimens is available, such as Sections 23 (Lawrence Quarry) and 15 (Calumet), there is a substantial range of mean tabularium dimensions. No locality stands out as significantly different from the others in these characters.

Septal length appears to be related to wall thickness, with long septa occurring only in those coralla that have thick corallite walls (Text-fig. 19D). These characters show some interlocality variation; septa are generally long at Section 23, and are variably developed at Section 15. Septal length and wall thickness do not correlate with tabularium dimensions.

Discussion.—These coralla are assigned to a new species, *Halysites alexandricus*. This species is the oldest representative of *Halysites* documented from North America. Worldwide, members of this genus are rare in uppermost Ordovician to lowest Silurian strata, but three other species have characters that are similar to those of *H. alexandricus*. The oldest definite member of this genus is *Halysites praecedens* Webby and Semeniuk (1969, pp. 349–353, figs. 2–6), from the upper Bowan Park Group and upper Canomodine Limestone of New South Wales, Australia (Ordovician, upper Caradoc–lower Ashgill; Webby *et al.*, 1981, pl. 1). It has tabularium dimensions of about 1.2–2.0 mm by 1.2–1.6 mm, rectangular tubules, and flat tabulae. *Halysites* sp. of Hall (1975, p. 89, fig. 12, pl. 5, figs. b, c), from the Uralba Beds of New South Wales (Upper Ordovician, Ashgill), has corallites with tabularium dimensions of about 1.4–1.7 mm by 0.8–1.0 mm, arranged in short ranks. *Halysites priscus* Klaamann (1966, p. 93, pl. 22, figs. 5–7), from the Juuru Stage of Estonia (lower Lower Silurian, Lower Llandovery), has tabularium dimensions of 1.6–1.8 mm by 1.4–1.55 mm, and rectangular tubules. All three of these species differ from *H. alexandricus* by having smaller or absent corallite septa, much thinner walls between corallites



Text-figure 19.—Intraspecific variation in *Halysites alexandricus.* **A**, **B**, Tabularium size-frequency distributions for selected coralla: A, USNM 485781 (holotype), Section-interval 31-1 (Thebes North); B, USNM 485809, Section-interval 37-1 (Essex). Each graph represents a single transverse section; tabularium length and width are shown separately; n = number of tabularia, c.v. = coefficient of variation. **C**, Relationship between mean tabularium width and mean tabularium length for transverse sections from 20 coralla; H = USNM 485781 (holotype). **D**, Relationship between length of septa as a percentage of tabularium radius and mean wall thickness for transverse sections from 11 coralla. Symbols for Section-intervals in C and D: □ 23a-1, 23-2 (Lawrence Quarry); + 31-1 (Thebes North); ○ 15-1 (Calumet); △ 37-1 (Essex); ■ all other Section-intervals.

and tubules, and tubules that are more abundant and that were initiated lower in the growth of the adjacent corallites.

Patterns of increase observed in *H. alexandricus* are notable for their variability (see *Astogeny and corallite increase,* above). Interstitial increase through expansion of an existing tubule is consistent with forms described from Ordovician and Silurian species of *Halysites* by Webby and Semeniuk (1969, pp. 354, 355, fig. 8a) and by Webby (1975, p. 35, fig. 5), but the connections between corallite lumina in one specimen of *H. alexandricus* suggest that axial increase (*cf.,* Lee and Elias, 1991, p. 193, figs. 1, 2) may also have occurred. Lateral increase took place either with or without an intervening tubule; the former pattern is the same as that reported by Webby and Semeniuk (1969, p. 355, fig. 8b) and Webby (1975, p. 34, fig. 4) for Ordovician and Silurian species of *Halysites,* whereas the latter was suggested by Buehler (1955, p. 14) and Hamada (1959, p. 276) as the most likely mode of increase for all halysitids. The occurrence of this range of types of increase in one species indicates that it could vary styles of growth, probably in response to local conditions.

"Megacorallites," which occur rarely in *H. alexandricus,* are apparently rare among halysitid corals in general. They have been previously reported in two specimens of *Catenipora* from the Lang River Formation (Upper Ordovician) on Somerset Island in the Canadian Arctic. The "megacorallites" in one corallum from Somerset Island are mostly subcircular in transverse section, and commonly occur at the center of tri- or quadripartite rank divergences (Dixon, 1976, pl. 1, figs. 1, 2a, 2b). "Megacorallites" in the other specimen are more commonly subelliptical, and occur within uniserial ranks (Dixon, 1976, pl. 1, figs. 3, 4a–

c). The paleobiologic significance of "megacorallites" is uncertain (see Dixon, 1976, p. 918). We consider them to be anomalous features; as such they are not given weight in taxonomy (*cf.*, Dixon, 1976, p. 920).

Halysites alexandricus was listed and illustrated by Elias and Young (1992, figs. 2, 3e, 3f, tables 1, 2) as *Halysites* n. sp. A. A similar younger species, *Halysites* sp. cf. *H. alexandricus* from the Sexton Creek Limestone of southern Illinois, is described below.

Occurrences.—Uppermost Ordovician (Gamachian): Cason Shale, western north-central Arkansas; Leemon Formation, southern Illinois and southeastern Missouri. Uppermost Ordovician (Gamachian) to lowermost Silurian (?; Lower Llandovery?, lower Rhuddanian?): lower and upper Keel Formation, south-central Oklahoma. Uppermost Ordovician (?; Gamachian?) to lowermost Silurian (Lower Llandovery, lower Rhuddanian): Wilhelmi Formation, northeastern Illinois; lower Mosalem Formation, northwestern Illinois. Lowermost Silurian (?; Lower Llandovery?, lower Rhuddanian?): Kissenger Limestone Member, Bryant Knob Formation, northeastern Missouri.

Holotype.—USNM 485781 (Pl. 10, figs. 2–4), interval 31-1, Leemon Formation, Section 31 (Thebes North), Alexander County, Illinois.

Paratypes.—Four specimens: USNM 485782 (Pl. 9, figs. 1–3), site 23i, USNM 458778 (Pl. 9, figs. 4–6), site 23ii, interval 23-2 (*Brevilamnulella* beds), Keel Formation, Section 23 (Lawrence Quarry), Pontotoc County, Oklahoma; USNM 485783 (Pl. 10, figs. 7, 8), interval 15-1, Kissenger Limestone Member, Bryant Knob Formation, Section 15 (Calumet), Pike County, Missouri; UI X-8723 (Pl. 11, figs. 5, 6), collected by T. E. Savage (labelled "*Halysites catenularia,* 1 mi. below otc. of Channahon ls."), Wilhelmi Formation, 3.2 km south of Channahon, Will County, Illinois.

Other material described above.—38 specimens: USNM 485779a, 485784, site 23iii, USNM 485780a, 485785b, 485786, site 23iv, interval 23-2 (*Brevilamnulella* beds), USNM 485787, 485788, site 23i, USNM 485789, 485790, site 23ii, interval 23-3, USNM 423421 (paratype of *Keelophyllum oklahomense* is attached to *Halysites alexandricus*), 485791, 485792, collected by R. J. Elias and R. J. McAuley in 1983, interval 23a-1 of McAuley and Elias (1990, p. 53, fig. 2), Keel Formation, Section 23 (Lawrence Quarry), Pontotoc County, Oklahoma; USNM 485793, interval 24-3, Keel Formation, Section 24 (Coal Creek), Pontotoc County, Oklahoma; USNM 485794, interval 25-1, Keel Formation, Section 25 (Hunton), Coal County, Oklahoma; USNM 485795, collected by W. W. Craig, interval 33-1, Cason Shale, Section 33 (Buffalo River), Searcy County, Arkansas; USNM 485796, interval 31-1, Leemon Formation, Section 31 (Thebes North), Alexander County, Illinois; UI C-886b, collected by T. E. Savage (labelled "Edgewood [Formation], near Gale, Ill."), Leemon Formation, Gale Section, Alexander County, Illinois; USNM 423401 (*H. alexandricus* is in matrix enclosing *Streptelasma leemonense*), collected by R. J. Elias and R. J. McAuley in 1983, interval 20-3, Leemon Formation, Section 20 (Short Farm), Cape Girardeau County, Missouri; USNM 485797, interval 18-2, USNM 485723c, interval 18-3, Kissenger Limestone Member, Bryant Knob Formation, Section 18 (Kissenger), Pike County, Missouri; USNM 485727b, 485798, 485799, 485800a, 485800b, 485801–485803, interval 15-1, Kissenger Limestone Member, Bryant Knob Formation, Section 15 (Calumet), Pike County, Missouri; USNM 485804, 485805, interval 14-1, Kissenger Limestone Member, Bryant Knob Formation, Section 14 (Higginbotham Farm), Pike County, Missouri; USNM 485806–485809, interval 37-1, Wilhelmi Formation, Section 37 (Essex), Kankakee County, Illinois; UI C-157, collected by H. F. Crooks (labelled "*Halysites catenulatus,* loc. A-1c"), UI C-1587b, collected by T. E. Savage (labelled "*Halysites catenularia,* 1 mi. below otc. of Channahon ls."), Wilhelmi Formation, 3.2 km south of Channahon, Will County, Illinois; USNM 485810, 485811, interval 32-1z, Mosalem Formation, Section 32 (Thomson East), Carroll County, Illinois.

Halysites species cf. **H. alexandricus**, new species
Plate 11, figures 7–9

Description.—Ranks are moderately long, consisting of one to six corallites. They are straight or broadly curved, and moderately constricted at intercorallites. Rank junctions occur at lateral corallite walls, or very rarely at tubules. Lacunae are broad, elongate or subpolygonal (Pl. 11, fig. 7). In transverse section, corallites are subelliptical, with tabularium dimensions commonly having length 1.25–1.55 mm and width 0.75–0.90 mm (Table 18). Where a rank junction occurs along a lateral corallite wall, the junction corallite is usually distorted in the direction of the side rank (Pl. 11, fig. 8). In longitudinal section, corallites are straight or slightly curved (Pl. 11, fig. 9).

Corallite walls are thick, averaging about 0.2 mm (Table 18). They are composed of two layers: a thinner, dark outer layer and a thicker, pale inner layer. Microstructure could not be determined because of recrystallization. Walls between tabularia and tubules are thick; where tubules are absent, walls between adjacent tabularia are very thick (Pl. 11, fig. 7). Septal spines are slender and long, averaging 48% of tabularium radius (Table 18). Tabulae are flat to strongly concave, usually complete, and irregularly and densely spaced, averaging about 12 in 5 mm (Table 18).

In transverse section, tubules are usually subelliptical and are very small, measuring 0.1–0.2 mm by 0.1–0.2 mm (Table 18). Most tubules are infilled with skeletal material. A tubule does not occur between every pair of adjacent corallites. Lateral walls of tubules are thick. Tubules are not seen in longitudinal section (Pl. 11, fig. 9).

Discussion.—This corallum bears a high degree of similarity to the older *Halysites alexandricus,* which occurs in uppermost Ordovician and lowermost Silurian rocks of the east-central United States. This similarity probably reflects an ancestor–descendent relationship. The only significant difference between these forms is that tabulae in this corallum are commonly strongly concave and are more closely spaced than in any specimen of *H. alexandricus* (see Table 18). Tabularium dimensions in this corallum are smaller than those of most specimens of *H. alexandricus,* but still within the range for the latter species (see Text-fig. 20).

This corallum is identified as *Halysites* sp. cf. *H. alexandricus* because of the close similarity to *H. alexandricus,* as discussed above. The single specimen does not provide sufficient information for recognition of a new species. It was referred to as *Halysites* sp. cf. *H.* n. sp. A by Elias and Young (1992, fig. 2).

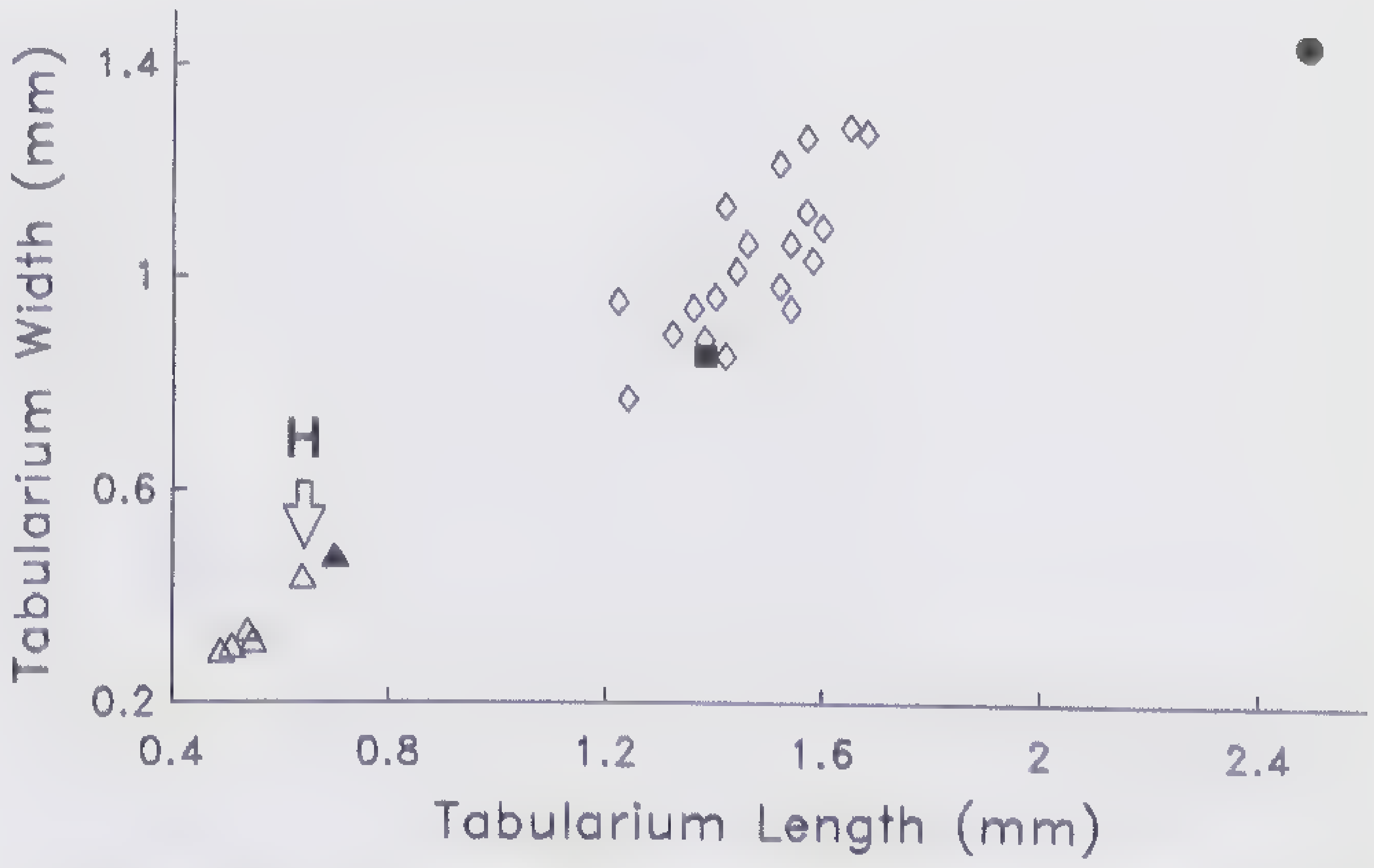
Occurrence.—Lower Lower Silurian (Lower? Llandovery, upper Rhuddanian?): Sexton Creek Limestone, southern Illinois.

Material described above.—One specimen: UI C-1346a, collected by T. E. Savage (labelled "*Halysites catenulatus*"), Sexton Creek Limestone, Sexton Creek, Alexander County, Illinois.

Halysites? species A
Plate 12, figures 1, 2

Description.—Ranks are moderately long, consisting of one to more than four corallites. Ranks are straight or slightly curved, and moderately constricted at intercorallites; they surround broad, subpolygonal lacunae. Rank junctions occur at lateral corallite walls. In transverse section, corallites are subelliptical and large, with tabularium dimensions commonly having length 2.3–2.7 mm and width 1.3–1.6 mm (Table 18). A corallite having a rank junction along its lateral wall is usually distorted in the direction of the side rank (Pl. 12, fig. 1).

Corallite walls are thick, about 0.2 mm (Table 18); microstructure cannot be determined because of recrystallization. Intercorallites are very thick in the direction of rank extension. Septal spines are common to abundant, upturned, thick, and of medium length, averaging 28% of tabularium radius (Table 18; Pl. 12, fig. 2). Tabulae are flat or irregular, mostly complete, and of variable thickness, with some being quite thick (Pl. 12, fig. 2). Tabulae are closely spaced, averaging about 11 in 5 mm (Table 18). Some tabulae bear short to long, vertically oriented spines on their upper surfaces; spines are most abundant on thickened tabulae (Pl. 12, fig. 2).



Text-figure 20.—Relationship between mean tabularium width and mean tabularium length in halysitid species from the east-central United States. Symbols for species: ◇ *Halysites alexandricus;* n (number of coralla) = 20; ■ *Halysites* sp. cf. *H. alexandricus;* n = 1; ● *Halysites*? sp. A; n = 1; △ *Catenipora lawrencica;* Section 23 (Lawrence Quarry); n = 5; H = USNM 485780b (holotype); ▲ *C. lawrencica;* Section-interval 14-1 (Higginbotham Farm); n = 1.

Tubules are not observed. The central parts of many intercorallites, however, have the appearance of small, broad tubules that have been filled in, either by the growth of skeletal material or by recrystallization (Pl. 12, fig. 1).

Discussion.—Assignment of this corallum to *Halysites* is questionable because open tubules were not observed between the corallites. Nevertheless, the structures that are present in the intercorallite walls may represent tubules that were filled in during later skeletal growth or by recrystallization. In the past, some species with intercorallites of similar character have been placed in *Catenipora;* a revision of these genera is needed to determine where the boundary between them should be placed (see *Discussion* under *Halysites,* p. 67).

This corallum is similar to Silurian halysitids that have been assigned by different authors to *Halysites gotlandicus* Yabe (1915) (= *Catenipora gotlandica*). The original description of *H. gotlandicus* from Korpklint, Gotland, Sweden (probably Upper Visby or Högklint beds: upper Lower Silurian, Lower Wenlock; Laufeld and Jeppsson, 1976, fig. 1), indicates that it has large corallites with dimensions of 1.9–2.1 mm by 1.6–1.7 mm, and short septal spines, but lacks tubules (Yabe, 1915, pp. 34(10), 35(11), pl. 7(3), figs. 1, 2; Buehler, 1955, p. 57). Yabe's illustrated transverse section, however, appears to show tubules that have been filled with skeletal material.

Catenipora cf. *gotlandica* of Klaamann (1966, pp. 41, 42, fig. 18, pl. 6, fig. 6), from the Juuru Stage of Estonia (lower Lower Silurian, Lower Llandovery), is most similar to our corallum. It has irregular tabulae, some of which have spines on their surfaces, and well-developed septal spines, but differs by having smaller corallites with dimensions of about 1.7–2.0 mm by 1.3–1.5 mm (inside?), and smaller intercorallites that probably lack infilled tubules. *Catenipora gotlandica,* as described and illustrated by Klaamann (1966, pp. 42, 43, fig. 19) from the Upper Llandovery of Gotland, the Juuru Stage of Estonia, and the Llandovery to Wenlock of Arctic Russia and the Siberian Platform, is less similar. It has intercorallites that are short in the direction of rank extension, and lacks tabular spines.

Catenipora gotlandica was described and illustrated from the mid-Llandovery Brassfield Formation of Ohio by Laub (1979, pp. 290–295, pl. 9, fig. 8, pl. 33, figs. 1, 2, pl. 42, fig. 2). It has smaller corallites than our corallum, with dimensions of 1–2 mm by 1.2 mm, and smaller intercorallites, but has large septa and appears to have sporadically developed infilled tubules.

The corallum we describe here is clearly differentiated from the other halysitid species occurring in the study region by its much larger corallite dimensions (Text-fig. 20). It is identified as *Halysites*? sp. A because of the problems outlined above, and because only one fragmentary specimen was found. *Halysites*? sp. A was referred to as *Halysites* sp. A by Elias and Young (1992, fig. 2).

Occurrence.—Lower Lower Silurian (Lower? Llandovery, upper Rhuddanian?): Sexton Creek Limestone, southern Illinois.

Material described above.—One specimen: UI C-1346b, collected by T. E. Savage (labelled "*Halysites catenulatus*"), Sexton Creek Limestone, Sexton Creek, Alexander County, Illinois.

Genus **Catenipora** Lamarck, 1816

Catenipora Lamarck, 1816, p. 206.
Palaeohalysites Chernyshev, 1941, p. 36.
Quepora Sinclair, 1955, p. 96.
[?] *Eocatenipora* Hamada, 1957, p. 398.

Type species.—By subsequent designation (Lang *et al.,* 1940, p. 33): *Catenipora escharoides* Lamarck (1816, p. 207); Silurian, Gotland, Sweden.

Diagnosis.—Halysitidae with circular to elliptical corallites arranged in uniserial ranks. Septa consist of longitudinal ridges and/or rows of spines; may be absent. All or most corallite tabulae are complete. Tubules are absent.

Remarks.—The concept of *Catenipora* used here is similar to that of Laub (1979, pp. 288–290). We follow him in the synonymization of *Palaeohalysites* and *Quepora,* and the questionable synonymization of *Eocatenipora.* Problems associated with the distinction of *Catenipora* from *Halysites* are addressed elsewhere (see *Discussion* under *Halysites,* p. 67).

Catenipora lawrencica, new species
Plate 12, figures 3–11

Derivation of name.—The species name is derived from the type locality, Section 23 (Lawrence Quarry), Pontotoc County, Oklahoma.

Diagnosis.—*Catenipora* with ranks usually of one to four corallites; most rank junctions occur at intercorallites. Tabularium dimensions commonly with length 0.4–0.7 mm, width 0.3–0.5 mm. Ranks strongly constricted at intercorallites. Corallite walls thick, septal spines common. Tabulae are complete.

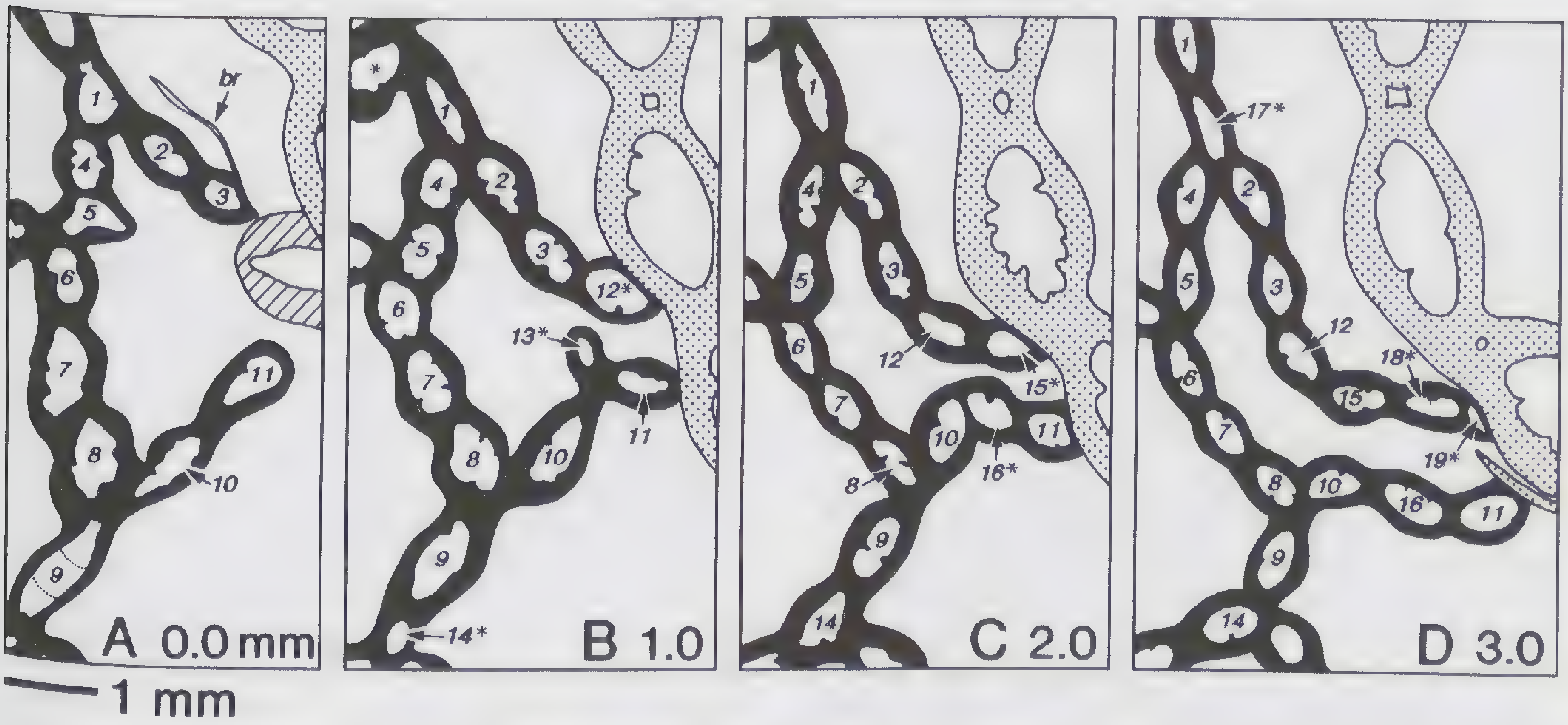
Description of coralla.—Coralla are small, and commonly occur as encrusters on *Halysites alexandricus.* Growth forms cannot be determined since all specimens are bound in matrix.

Ranks commonly consist of one to four corallites, but are longer in some cases (Pl. 12, figs. 5, 10, 11). Ranks are broadly curved and strongly constricted at intercorallites. They enclose lacunae that are small and polygonal to subpolygonal, or elongate, narrow, and sinuous in some places. Rank junctions usually occur at intercorallites (Pl. 12, fig. 5), but may occur at lateral corallite walls (Pl. 12, fig. 10). In transverse section, corallites are subelliptical or subovate, with flat or rounded ends at intercorallites (Pl. 12, figs. 6, 10, 11). They are small, with tabularium dimensions commonly having length 0.4–0.7 mm and width 0.3–0.5 mm (Table 18). Corallites are straight, curved, or slightly geniculate in longitudinal section (Pl. 12, figs. 3, 7).

Corallite walls are thick, usually 0.1–0.2 mm (Table 18). Walls are composed of two layers: a thinner, dark outer layer and a thicker, pale inner layer (Pl. 12, fig. 9). Microstructure cannot be determined because of recrystallization. Intercorallite walls are thin to moderately thick. In transverse section, the central part of an intercorallite in some cases comprises a dark transverse line (Pl. 12, fig. 9). Septa consist of moderately thick spines, with length averaging 19% of corallite radius (Table 18); they are common where preserved (Pl. 12, fig. 6). In longitudinal section, septal spines are arranged in rows (Pl. 12, fig. 3).

Tabulae are flat, slightly concave or slightly convex, and complete (Pl. 12, figs. 3, 7). Spacing is variable but moderately close, averaging about 13 tabulae in 5 mm (Table 18). Tabulae were probably thin prior to recrystallization.

Astogeny and corallite increase.—Most observations are based on one serial-sectioned corallum (holotype



Text-figure 21.—**A–D**, Serial transverse sections illustrating corallite increase in a corallum of *Catenipora lawrencica;* USNM 485780b (holotype), Section-interval 23-2 (Lawrence Quarry) (see also Pl. 12, figs. 3–6). Corallite walls and septa are solid, tabulae are finely stippled; a rank of *Halysites alexandricus* is coarsely stippled, a possible corallite of *Aulopora* is hachured, *br* = brachiopod shell; scale bar is shown. Heights in mm are above an arbitrary datum within a mature part of the corallum; numbers in italics represent individual corallites; an asterisk indicates the first appearance of a particular corallite.

USNM 485780b). Other specimens are used for comparison.

The protocorallite is not known. The lowest known stages of corallum growth have thick-walled, septate corallites that are not distinguishable from those occurring higher up. Ranks in the lower part of the corallum are short and straight or slightly curved, commonly composed of one to three corallites. They are initially spreading and do not join to form lacunae. Higher in the corallum, ranks are subparallel, longer and more sinuous, commonly having two to four corallites. Ranks join to surround subpolygonal lacunae that become more elongate with height. The shape of ranks may vary depending on whether lateral growth was blocked by large skeletal grains (Text-fig. 21). In longitudinal section, some corallites extend through much of the height of the corallum.

Corallite increase may be interstitial (between adult corallites in a rank) or lateral (at the end or side of a rank). Interstitial increase apparently occurred through fission of the intercorallite wall. New corallites produced by interstitial increase are separated by thin walls from the adult corallites on either side (Text-fig. 21B, C, note corallites 10, 11, 16). In transverse section, such new corallites are initially more broadly elliptical, and are shorter in the long axis than are adult corallites; they expanded rapidly to adult size and shape (Text-fig. 21C, D, note corallite 16).

Lateral increase occurred at the free ends of ranks, more rarely at the sides of ranks. At the end of a rank, a new corallite appeared through the fission of the end wall of the parent individual (Text-fig. 21D, note corallite 19). The intercorallite wall between the new corallite and the parent is thin, but of normal appearance. New corallites in such locations expanded rapidly, both where rank ends were free and where they adhered to large skeletal grains (Text-fig. 21C, D). At the side of a rank, a new corallite is located beside an intercorallite (Text-fig. 21B, corallite 13).

Partial mortality of colony growth surfaces was not observed. A single corallite, however, viewed in longitudinal section, exhibits a constriction followed by rejuvenation from within the calice (Pl. 12, figs. 3, 4).

Discussion.—The coralla described above are assigned to a new species, *Catenipora lawrencica.* This is one of the older members of an important group of small-corallite *Catenipora* species that developed during an evolutionary radiation from the latest Ordovician through the earliest Silurian. Species in this group occur in Asia, central and eastern North America, and the Baltic region. All have tabularium dimensions of less than 1.5 mm by 1.2 mm and rank junctions occurring mostly at intercorallites, and many have well-developed septa and polygonal or broad lacunae. Although the shared characters allow these corals to be readily recognized as members of a group, the literature includes many names for what is probably a limited number of species; this prevents the compilation of a valid list at present.

Other than *Catenipora lawrencica,* the well-documented Ordovician members of this group all occur in Asia. These include *Catenipora* (*Catenipora*?) *minima* Yü (1960, pp. 83, 98, pl. 9, figs. 6, 7) from the Upper Ordovician of western Zhejiang Province, China, *Catenipora zhejiangensis* Yü as described by Lin and Chow (1977, pp. 160, 161, pl. 40, figs. 2, 3) from the Upper Ordovician (Ashgill) of Zhejiang and Jiangxi provinces, China, and *Catenipora capilliformis* Kokscharskaya (in Volkova *et al.,* 1978, pp. 30, 31, pl. 3, fig. 1) from the Upper Ordovician Barannskiy Stage of southern Verkhoyan, Siberian region, Russia. These three species are very similar to one another and may be conspecific; they are distinguished from *C. lawrencica* by their larger corallites with tabularium dimensions of about 0.6–0.9 mm by 0.5–0.8 mm, and a lower degree of constriction at each intercorallite.

Most of the many small-corallite *Catenipora* species described and illustrated from the Baltic region are from the lower Lower Silurian (Upper Llandovery) or upper Lower Silurian (Wenlock). Among the few earlier occurrences, *Catenipora escharoides* has been listed by Aarhus (1982, p. 44) from the latest Ordovician of the Oslo region, Norway. It also occurs in the upper Rytteråker Formation (Llandovery 7b: Upper Llandovery, Telychian; Worsley *et al.,* 1983, fig. 5) and in the lower and middle Vik Formation (Llandovery 7c: Telychian; Worsley *et al.,* 1983, fig. 5) of Ringerike, Norway (Aarhus, 1982, p. 44, pl. 2, fig. 6), and in the Lower and Upper Visby beds of Gotland, Sweden (uppermost Llandovery–Lower Wenlock; Laufeld and Jeppsson, 1976, fig. 4) (Stasinska, 1967, pp. 44, 45, pl. 3, figs. 5–8). *Catenipora escharoides* is differentiated from *C. lawrencica* by its much larger corallites with tabularium dimensions of about 1.0–1.5 mm by 0.9–1.2 mm, much larger septa, and small, regular lacunae. *Catenipora minuta* Stasinska (1967, p. 48, pl. 6, fig. 2), from the Upper Llandovery of Ringerike (Llandovery 7), is very similar to *C. escharoides* and may be conspecific with it.

Another early Baltic species is *Catenipora arctica* Chernyshev, as described and illustrated by Klaamann (1966, pp. 40, 41, pl. 22, fig. 8) from the Lower Llandovery Juuru Stage of Estonia. It has thick walls and subpolygonal lacunae, but is distinguished from *C. lawrencica* by its larger corallites with tabularium dimensions of 0.8–1.0 mm by 0.54–0.66 mm. *Catenipora arctica* also occurs in the Llandovery of Taimyr, northern Russia (Klaamann, 1966, p. 41).

Of the later members of the small-corallite *Catenipora* group from the Baltic, the species most similar to *C. lawrencica* is probably *Catenipora panga* Klaamann (1961; 1966, pp. 52, 53, pl. 14, figs. 7, 8), from the Adavere and Jaani stages of Estonia (Upper Llandovery–Wenlock). *Catenipora panga* also has constricted intercorallites and subpolygonal lacunae, but is distinguished from *C. lawrencica* by its larger corallites with tabularium dimensions of 0.9–1.1 mm by 0.7–0.8 mm, and irregular tabulae. *Catenipora jarviki* Stasinska (1967, pp. 47, 48, pl. 2, fig. 1), from the Wenlock of Gotland, Sweden (Visby beds?), is also similar to *C. lawrencica,* but has diamond-shaped corallites that are larger (tabularium dimensions 0.6–0.9 mm by 0.4–0.5 mm) and arranged in longer ranks.

Most of the described North American small-corallite *Catenipora* species are Late Llandovery or Wenlock. Bolton (1981a, pl. 1, figs. 4, 5), however, illustrated two coralla identified as *Catenipora* sp. from the Ellis Bay Formation of Anticosti Island, Québec (member 5 of Bolton: uppermost Ordovician, Gamachian; Petryk, 1981, fig. 4). These specimens possess polygonal to subpolygonal ranks and constricted intercorallites. They differ from *C. lawrencica* by having significantly larger corallites with long tabularium dimensions greater than 1 mm. Other coralla from the Ellis Bay Formation, Becscie Formation (Lower Llandovery, Rhuddanian), and Jupiter Formation (Middle–Upper Llandovery, upper Aeronian–Telychian; Barnes, 1988, fig. 2) on Anticosti Island were described as *Halysites catenularia micropora* Whitfield by Twenhofel (1928, p. 125). Twenhofel's material, deposited at the Geological Survey of Canada and the Yale Peabody Museum, is unfortunately lost (Bolton, written commun., 1991; White, written commun., 1991), but his description of corallites less than 1.0 mm by 0.5 mm suggests that it may have included specimens similar to *C. lawrencica.*

Six of the seven specimens of *C. lawrencica* are from the Keel Formation at Section 23 (Lawrence Quarry). These are very consistent with one another in most of the important morphologic characters, but they differ somewhat from the single fragmentary corallum from the Bryant Knob Formation at Section 14 (Higginbotham Farm). The latter specimen has larger corallites (Text-fig. 20), and also appears to have longer and thicker septa. These differences may be related to geographic and stratigraphic separation, and are not sufficient to place the specimen from Section 14 in another species. *Catenipora lawrencica* was referred to as *Catenipora* n. sp. A by Elias and Young (1992, fig. 2, tables 1, 2).

Occurrences.—Uppermost Ordovician (Gamachian): lower Keel Formation, south-central Oklahoma. Lowermost Silurian (?; Lower Llandovery?, lower Rhuddanian?): Kissenger Limestone Member, Bryant Knob Formation, northeastern Missouri.

Holotype.—USNM 485780b (Pl. 12, figs. 3–6), site 23iv, interval 23-2 (*Brevilamnulella* beds), Keel Formation, Section 23 (Lawrence Quarry), Pontotoc County, Oklahoma.

Paratypes.—Two specimens: USNM 485785c (Pl. 12, figs. 7–10), site 23iv, interval 23-2 (*Brevilamnulella* beds), Keel Formation, Section 23 (Lawrence Quarry), Pontotoc County, Oklahoma. USNM 485812b (Pl. 12, fig. 11), interval 14-1, Kissenger Limestone Member, Bryant Knob Formation, Section 14 (Higginbotham Farm), Pike County, Missouri.

Other material described above.—Four specimens: USNM 485813, site 23i, USNM 485779b, site 23iii, USNM 485814, site 23iv, interval 23-2 (*Brevilamnulella* beds), USNM 485815, collected by R. J. Elias and R. J. McAuley in 1983, interval 23a-1 of McAuley and Elias (1990, p. 53, fig. 2), Keel Formation, Section 23 (Lawrence Quarry), Pontotoc County, Oklahoma.

Order **FAVOSITIDA** Wedekind, 1937

Suborder **FAVOSITINA** Wedekind, 1937

Superfamily **FAVOSITICAE** Dana, 1846

Family **FAVOSITIDAE** Dana, 1846

Subfamily **FAVOSITINAE** Dana, 1846

ex Favositidae Dana, 1846, p. 116; *nom. transl.* Milne-Edwards and Haime, 1851, p. 230.
Palaeofavositinae Sokolov, 1950a, pp. 164, 165.
Paleofavositinae Sokolov, 1950a; *nom. correct.* Hill, 1981, p. F546.

Diagnosis.—Favositidae with septa spinose or absent. Longitudinal rows of pores located in wall faces and/or in corners.

Discussion.—The Paleofavositinae was previously distinguished from the Favositinae solely on the basis of pore position (Hill, 1981, pp. F541, F546); all other characters are similar between the nominate genera. Since pore form and placement are extremely variable within *Paleofavosites,* however, it is not feasible to continue to separate these subfamilies. Members of *Paleofavosites* may possess combinations of mid-wall pores, simple corner pores, and solenia (funnel-shaped corner pores), and it is probable that the transition from this genus to *Favosites* occurred independently in more than one lineage (see *Discussion* under *Paleofavosites,* p. 78).

Most septal spines in *Paleofavosites subelongus* appear to be composed of bundles of subparallel fibers, rather than being truly trabecular in form (see *Microstructure* under *P. subelongus,* p. 83). This appearance supports the observations of Schouppé and Oekentorp (1974, p. 167) on favositid septal form, and is not consistent with Sokolov's (1955, p. 28) and Hill's (1981, p. F448) idea that tabulatan septal spines are fine trabeculae.

Genus **PALEOFAVOSITES** Twenhofel, 1914

Calamopora Goldfuss, 1829, p. 77.
Paleofavosites Twenhofel, 1914, p. 24; 1928, p. 125; Poulsen, 1941, p. 20; Stearn, 1956, pp. 59, 60; Hill, 1959, p. 11; Flower, 1961, pp. 71–73; Scrutton, 1975, pp. 29, 30; Oekentorp, 1976, p. 165; Powell and Scrutton, 1978, pp. 312, 313; Laub, 1979, pp. 259–263; Hill, 1981, pp. F546, F547; Scrutton, 1985, p. 34.
Multisolenia Fritz, 1937, p. 231; Sokolov, 1950b, pp. 221, 222; 1951b, p. 50; Hill and Stumm, 1956, p. F464; Stearn, 1956, p. 65; Klaamann, 1964, p. 42; Stel, 1975, p. 61.
Palaeofavosites Twenhofel, 1914. Lang *et al.,* 1940, p. 94; Sokolov, 1950b, p. 216; 1951a, pp. 30, 31; 1951b, p. 12; Hill and Stumm, 1956, p. F461; Nelson, 1963, p. 51; Sokolov and Tesakov, 1963, pp. 39, 40; Klaamann, 1964, p. 5; Stasinska, 1967, p. 66; Oekentorp, 1971, pp. 158, 159; Hall, 1975, p. 86; Stel, 1975, p. 41.
Mesofavosites Sokolov, 1951b, pp. 59–61; Klaamann, 1964, p. 45; Stasinska, 1967, p. 76; Stel, 1975, p. 65.
Mesosolenia Mironova, 1960, p. 95.
Priscosolenia Sokolov, 1962, p. 58; Klaamann, 1964, p. 40; Stasinska, 1967, p. 73; Stel, 1975, p. 55.
Sparsisolenia Stasinska, 1967, p. 74.

Type species.—By original designation: *Favosites aspera* d'Orbigny (1850, p. 49); Aymestry Limestone (lower Upper Silurian, Ludlow), Leinthall Earls, Welsh Borderland, U.K. (Powell and Scrutton, 1978, p. 313).

Diagnosis.—Favositinae with contiguous polygonal corallites. Corner pores are characteristic; may be simple or take the form of solenia; a simple pore generally connects two corallites, may very rarely connect three corallites at a triple junction. Mid-wall pores may be present. Septa may be absent, or represented by variably developed spines arranged in vertical rows. Tabulae usually complete.

Discussion.—Twenhofel (1914, p. 24) based his original definition of *Paleofavosites* on material from Anticosti Island, Québec. He stated that *Favosites aspera* should be the type species because he thought at that time that *Paleofavosites prolificus* (Billings) and *Paleofavosites capax* (Billings) from Anticosti Island were junior synonyms of that species. Although Twenhofel (1928, p. 125) later changed this view, stating that *P. prolificus* should be the type species, *Paleofavosites asper* has been accepted as the type by all subsequent workers. This sequence of events is fortunate, since the holotype of *P. prolificus* is now known to be lost (Bolton, written commun., 1991); the lack of a type for such an important taxon could have caused considerable confusion.

Our concept of *Paleofavosites* follows the broad approach to this genus advocated by Stel and Oekentorp (1976, pp. 163–173) and Powell and Scrutton (1978, pp. 307, 308, 310, 312, 313). Like those authors, we consider genera possessing solenia (funnel-shaped corner pores) to be junior synonyms of *Paleofavosites.* These genera include *Multisolenia, Mesosolenia, Priscosolenia,* and *Sparsisolenia.* Stel and Oekentorp (1976, p. 173) suggested that, although *Multisolenia* and similar taxa are clearly congeneric with *Paleofavosites,* their solenid habit warrants placement in a distinct subgenus. Such a separation may be deemed reasonable in the future, but at present relationships among the different forms are too poorly understood for it to have any validity. The proposal by Stel and Oekentorp (1976, p. 173) that such a subgenus be named *Paleofavosites* (*Desmidopora*) should not be followed, as it was based on the incorrect interpretation of *Desmidopora* Nicholson as a subjective synonym of *Multisolenia. Desmidopora* is now considered to be a chaetetid (Stel and Oekentorp, 1980, pp. 407, 408; Hill, 1981, p. F515) or a sclerosponge (Scrutton, 1987, p. 488).

Powell and Scrutton (1978, pp. 307, 310) suggested that *Mesofavosites* should be considered a junior synonym of *Paleofavosites. Mesofavosites* was initially distinguished from *Paleofavosites* because it possesses both corner and mid-wall pores. As Powell and Scrutton noted, however, both forms of pore occur in the type species of *Paleofavosites,* and therefore both are characteristic of that genus. Corals having both corner and mid-wall pores are intermediate in evolutionary and stratigraphic position between *Paleofavosites* and *Favosites,* but it is possible that the transition in pore character occurred independently in more than one lineage at about the same time (Stearn, 1956, pp. 59, 60; see *Paleofavosites subelongus,* p. 40; *Discussion* under *Paleofavosites* sp. cf. *P. subelongus,* p. 91, and under *Paleofavosites adaensis,* p. 94). If such parallel evolution can be clearly demonstrated by future work, then it will be necessary either to synonymize *Paleofavosites* with *Favosites* or to define a new genus or genera based on characters other than pore position.

Our concept of *Paleofavosites* includes one character that was not accepted by some previous authors. Oekentorp and Schouppé (1969, p. 89) and Hill (1981, p. F547) stated that each corner pore opens into two corallites only. The material of *P. subelongus* that we examined includes one specimen that possesses an unequivocal three-way corner pore occurring at a triple wall junction (USNM 485877; Pl. 17, fig. 2), and other less well-preserved examples that may represent the same type of structure.

Paleofavosites subelongus (Savage, 1913)

Plate 13, figures 1–11; Plate 14, figures 1–11;
Plate 15, figures 1–12; Plate 16, figures 1–13;
Plate 17, figures 1–7

Favosites subelongus Savage, 1913, p. 64, pl. 3, figs. 9, 10; 1917, p. 114, pl. 5, figs. 9, 10.

Calapoecia favositoidea Savage, 1913, pp. 64, 65, pl. 3, figs. 1–3; 1917, p. 115, pl. 5, figs. 1–3.

[*cf.*] *Palaeofavosites forbesiformis* Sokolov, 1951b, pp. 28, 29, pl. 8, figs. 1, 2; Stasinska, 1967, pp. 68, 69, pl. 16, figs. 1a, 1b, table 4.

[*cf.*] *Palaeofavosites prolificus* (Billings, 1865). Nelson, 1963, p. 52, pl. 7, fig. 5.

[?] *Paleofavosites* sp. cf. *P. forbesiformis* Sokolov, 1951b. Bolton, 1981a, pl. 2, figs. 3, 4, pl. 3, figs. 9, 10.

Paleofavosites subelongus (Savage, 1913). Elias and Young, 1992, figs. 3a, 3b; Young and Elias, 1993, pl. 1, figs. 1–4, 11–16.

Diagnosis.—*Paleofavosites* with corallites of variable size; average adult corallite dimensions commonly 1.0–3.2 mm. Corallites usually have three to eight or nine sides. Walls straight, slightly wavy, or broadly curved in transverse section. Corner pores common, mid-wall pores extremely rare. Septa rod-like or thorn-like; of variable length, may be absent. Tabulae thin, flat or wavy, slightly concave or convex.

Description of coralla.—Coralla have low and high bulbous (Pl. 14, fig. 10), low and high domical (Pl. 16, fig. 5), and low columnar growth forms (Table 14). Size range is 14–77 mm wide and 9–68 mm high.

In transverse section, corallites are polygons of regular or irregular shape. Average corallite dimensions are extremely variable, 0.25–3.50 mm; average dimensions of adult corallites are commonly 1.0–3.2 mm (Table 19). Mean corallite areas on transverse sections are about 1–6 mm^2 (Table 19). Corallites usually have three to eight or nine sides, rarely up to 10 or 11 sides (Table 19). Distribution of corallite shapes is variable; where corallite sizes are regular, most corallites have five to seven sides (Pl. 15, fig. 7), but where the corallite size range is large, adult corallites with seven to nine sides are surrounded by small corallites with three or four sides (Pl. 15, figs. 11, 12, Pl. 16, fig. 1; see *Intraspecific variation,* below). In longitudinal section, corallites near the colony axis are straight; those occurring laterally are curved away from the axis (Pl. 14, fig. 10, Pl. 16, figs. 5, 12).

Corallite walls are usually straight or slightly wavy in transverse section (Pl. 13, figs. 1, 3). Walls may be broadly curved or bowed in some places (Pl. 13, fig. 1, Pl. 17, fig. 1). Wall thickness is commonly 0.05–0.20 mm (Table 19), and may vary cyclomorphically. The wall may appear to undulate between offset septa (Pl. 14, fig. 5, Pl. 16, fig. 7). In longitudinal section, walls are straight or wavy (Pl. 13, fig. 9, Pl. 14, fig. 3). Corner pores are common and irregularly distributed. Most corner pores are simple, with diameters com-

Table 19.—*Biometric data for favositids from the east-central United States. ACD = average corallite dimensions (all corallites and those having 6+ sides), CoA = corallite area, Pol = polygonality (number of sides), WT = wall thickness, LS = length of septa, PoD = pore diameter (corner pores only), Ta5 = number of tabulae in 5 mm, Se5 = number of septa in 5 mm, TC = thickness of cycles; s.d. = standard deviation, c.v. = coefficient of variation.*

species	*parameters*									
data	*ACD (all)*	*ACD (6+)*	*CoA*	*Pol*	*WT*	*LS*	*PoD*	*Ta5*	*Se5*	*TC*
Paleofavosites subelongus										
mean	1.62 mm	2.07 mm	2.72 mm^2	5.6	0.123 mm	21%	0.135 mm	4.5	19.8	13.5 mm
range of colony means	0.81–2.49 mm	1.11–2.99 mm	0.88–6.25 mm^2	4.9–6.1	0.050–0.210 mm	0–48%	0.095–0.205 mm	2.4–10.9	15.5–27.5	13.0–14.0 mm
s.d. of colony means	0.38 mm	0.46 mm	1.14 mm^2	0.3	0.038 mm	10%	0.025 mm	1.4	4.8	0.7 mm
c.v. of colony means	23.5	22.2	41.9	5.4	30.9	47.6	18.3	31.7	24.2	5.2
minimum	0.25 mm	0.85 mm	—	3	0.025 mm	—	0.050 mm	1	12	—
maximum	3.50 mm	3.50 mm	—	11	0.450 mm	—	0.300 mm	12	30	—
mean intracolony c.v.	35.5	13.2	—	27.0	20.0	—	20.2	20.1	10.0	—
no. of coralla studied	102	102	82	102	58	47	32	79	5	2
Paleofavosites sp. cf. *P. subelongus*										
mean	1.65 mm	2.06 mm	2.90 mm^2	5.8	—	—	0.150 mm	4.9	—	—
range of colony means	1.19–1.98 mm	1.68–2.46 mm	2.13–3.92 mm^2	5.0–6.1	—	—	—	4.0–5.8	—	—
s.d. of colony means	0.27 mm	0.28 mm	0.81 mm^2	0.4	—	—	—	1.3	—	—
c.v. of colony means	16.4	13.6	27.9	6.9	—	—	—	26.5	—	—
minimum	0.38 mm	1.25 mm	—	3	—	—	0.100 mm	2	—	—
maximum	3.00 mm	3.00 mm	—	12	—	—	0.200 mm	14	—	—
mean intracolony c.v.	33.6	11.1	—	28.9	—	—	28.0	18.5	—	—
no. of coralla studied	7	7	5	7	—	—	1	2	—	—
Paleofavosites adaensis										
mean	3.55 mm	4.04 mm	11.30 mm^2	6.0	0.049 mm	0	0.205 mm	4.7	—	—
range of colony means	3.05–4.11 mm	3.32–5.28 mm	7.69–17.40 mm^2	5.8–6.2	0.032–0.070 mm	0–0	—	2.2–8.1	—	—
s.d. of colony means	0.45 mm	0.70 mm	4.03 mm^2	0.1	0.016 mm	0	—	2.4	—	—
c.v. of colony means	12.7	17.3	35.6	1.7	32.7	0	—	51.1	—	—
minimum	0.58 mm	2.25 mm	—	3	0.025 mm	—	0.100 mm	1	—	—
maximum	5.82 mm	5.82 mm	—	10	0.100 mm	—	0.325 mm	10	—	—
mean intracolony c.v.	28.0	10.5	—	20.5	26.0	—	31.0	22.6	—	—
no. of coralla studied	7	7	6	7	4	4	1	6	—	—
Paleofavosites sp. cf. *P. ivanovi*										
mean	2.55 mm	3.30 mm	5.67 mm^2	5.8	0.069 mm	4%	0.121 mm	1.8	—	—
range of colony means	2.49–2.61 mm	3.26–3.35 mm	5.19–6.15 mm^2	5.7–5.9	—	—	—	—	—	—
s.d. of colony means	0.08 mm	0.06 mm	0.68 mm^2	0.1	—	—	—	—	—	—
c.v. of colony means	3.1	1.8	12.0	1.7	—	—	—	—	—	—
minimum	0.50 mm	2.58 mm	—	3	0.050 mm	—	0.075 mm	1	—	—
maximum	4.25 mm	4.25 mm	—	10	0.100 mm	—	0.175 mm	2	—	—
mean intracolony c.v.	34.0	10.7	—	28.4	23.2	—	27.3	10.7	—	—
no. of coralla studied	2	2	2	2	1	1	1	1	—	—
Paleofavosites sp. A										
mean	2.05 mm	2.34 mm	3.39 mm^2	5.9	0.086 mm	0%	—	4.1	—	18.5 mm
range of colony means	1.88–2.21 mm	2.20–2.47 mm	2.84–4.00 mm^2	5.6–6.3	—	—	—	3.0–6.2	—	—
s.d. of colony means	0.13 mm	0.11 mm	0.48 mm^2	0.3	—	—	—	1.3	—	—
c.v. of colony means	6.3	4.7	14.2	5.1	—	—	—	31.7	—	—
minimum	0.55 mm	1.82 mm	—	3	0.050 mm	—	—	2	—	—
maximum	2.82 mm	2.82 mm	—	9	0.125 mm	—	—	8	—	—
mean intracolony c.v.	26.4	9.8	—	22.2	32.6	—	—	27.6	—	—
no. of coralla studied	6	6	4	6	1	1	—	5	—	1

monly 0.08–0.25 mm (Table 19). The end of a wall adjacent to a pore is usually square and bulges slightly (Pl. 14, fig. 4, Pl. 16, fig. 11). Corner pores commonly have thin pore plates that are straight or are strongly curved into the lumina of corallites. Three-way corner pores, each connecting three adjacent corallites, occur rarely (Pl. 17, fig. 2). Where corallites are smaller, corner pores may take the form of solenia (funnel-shaped pores; Pl. 13, fig. 4, lower left side). In longitudinal section, solenia occur in regular rows. Mid-wall pores with diameters of about 0.10 mm occur rarely in a few coralla (Pl. 16, fig. 10; see *Paleofavosites subelongus*, p. 40).

In transverse section, septa are absent (Pl. 13, fig. 5, Pl. 15, fig. 7) to thick and thorn-like (Pl. 13, fig. 10), rod-like with square tips (Pl. 14, fig. 9, Pl. 15, fig. 11), or long and slender (Pl. 14, fig. 5). Septal length is variable, commonly up to 25% of corallite radius, but may be 50% of radius in newly initiated corallites (Table 19). In coralla with smaller than average corallites, septa are commonly rare or absent (Pl. 13, fig. 5). Where septa are well developed, a corallite contains as many septa as its size will allow; up to 37 septa in transverse section. In adjacent corallites, septa on opposite sides of a wall may be either opposed or alternating. In longitudinal section, septa may be straight and upwardly directed or horizontal, or may be downcurved adaxially; angles of septa in a single corallum may vary significantly in longitudinal section (Pl. 13, fig. 7, Pl. 16, fig. 6). Septal spines occur in rows that may change in number as septa are inserted with height in a corallite (Pl. 15, fig. 9); vertical spacing is 12–30 septal spines per 5 mm (Table 19). Septa are variably developed between coralla and between areas of a single corallum (Pl. 14, fig. 11, Pl. 15, fig. 2); in areas where tabulae are closely spaced cyclomorphically, septa may be very thick and abundant.

Tabulae are moderately thin. They are flat, wavy, or slightly concave or convex, and may curve upward laterally to meet the corallite wall (Pl. 13, fig. 2, Pl. 15, fig. 2). They are usually complete, very rarely incomplete (Pl. 16, fig. 12). The shapes of tabulae in transverse section indicate that they are often crenulate, with the arches of crenulations occurring near the corners of corallites (Pl. 14, fig. 1). In longitudinal section, tabulae are widely spaced, averaging about 4 in 5 mm (Table 19). In some coralla, tabular spacing varies cyclomorphically, with pairs of closely spaced and widely spaced bands of tabulae averaging 13.5 mm in thickness (Table 19; Pl. 14, fig. 10, Pl. 16, fig. 12). Tabulae are occasionally quite irregular in form, having lobe-like axial depressions or subcircular cavities axially (Pl. 14, figs. 2, 7). Tabulae hang from septal spines in some places (Pl. 14, fig. 6). They are often thickened where they connect with the corallite wall.

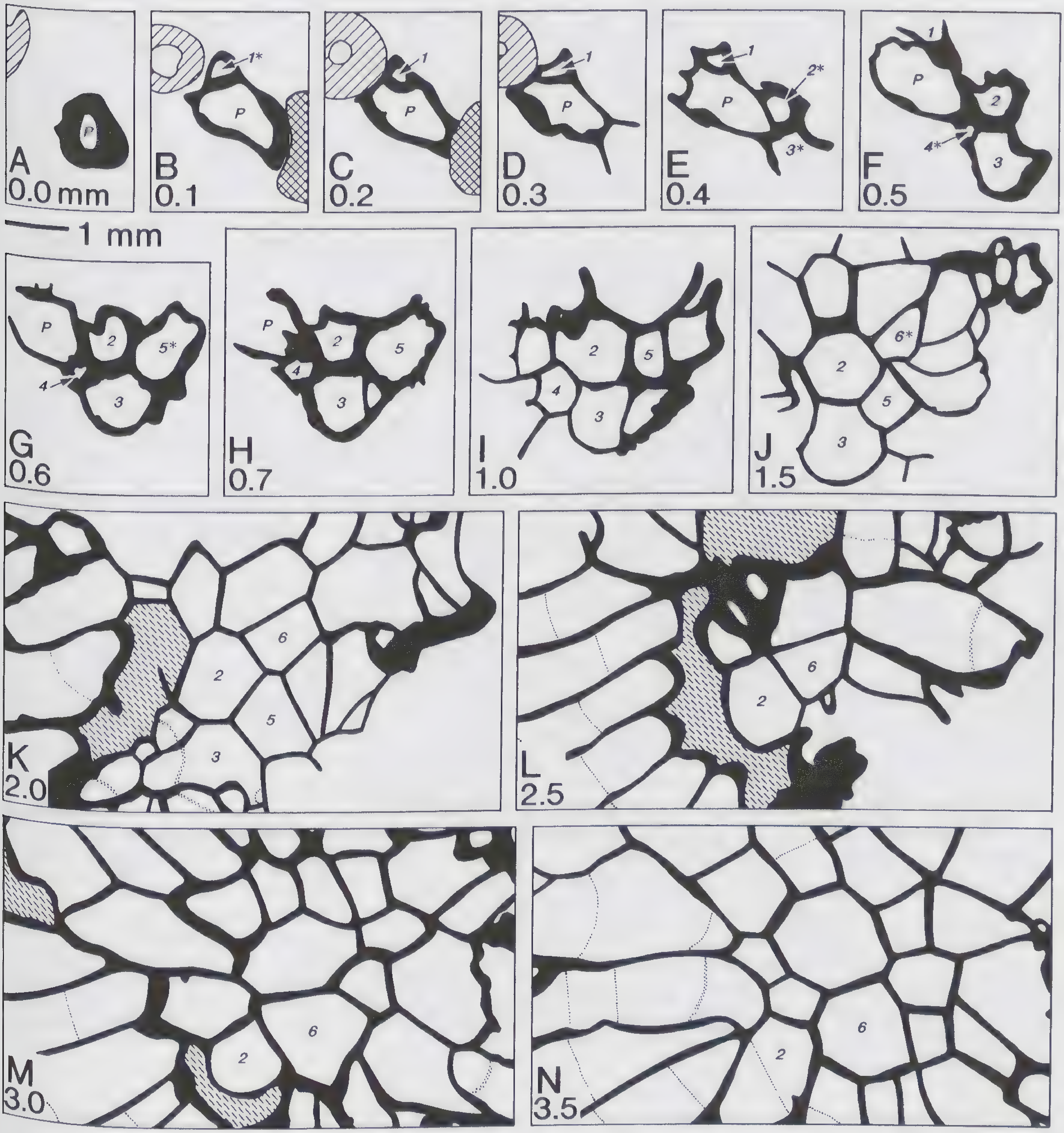
Astogeny and corallite increase.—Descriptions are based principally on four serial-sectioned coralla (USNM 459074, 459079, 459086, 485865) and one serial-sliced corallum (USNM 459080). Other specimens are used for comparison.

A full sequence of basal growth can be reconstructed in one serial-sectioned corallum (USNM 459086; Text-fig. 22). Initially, the protocorallite has a subovate lumen, an irregular external outline, and dimensions of 0.85 by 0.60 mm; it is thick-walled, apparently aseptate (Text-fig. 22A). The protocorallite is probably based on an algal grain. At about 0.1 mm above its base the protocorallite was joined by a small hysterocorallite; rapid offsetting followed, and by 0.5 mm above its base the corallum consisted of five corallites (Text-fig. 22B–F). Rare septa occur in the first 0.5 mm of the protocorallite; these are short, thick, and node-like. The protocorallite grew to a height of 0.7–0.8 mm prior to death. In its last complete section the protocorallite is oblique to the other individuals and has dimensions of 1.55 by 0.95 mm.

Several phases of lateral expansion and contraction occurred before the corallum was able to establish a spreading cerioid "base" at about 3.5 mm above the absolute base of the protocorallite (Text-fig. 22G–N). Through this growth phase, corallites have irregular shapes and sizes; the corallum axis is small, and divergence is often marked. Corallites positioned at the margins were commonly short-lived. At 3.5 mm above the absolute base, the larger corallites have average dimensions of about 1.3–1.7 mm, well within the range for adult corallites of this species. The corallite walls are thick, and septal spines are present. The later development of this corallum is typical of large-corallite variants of this species (see *Intraspecific variation*, below).

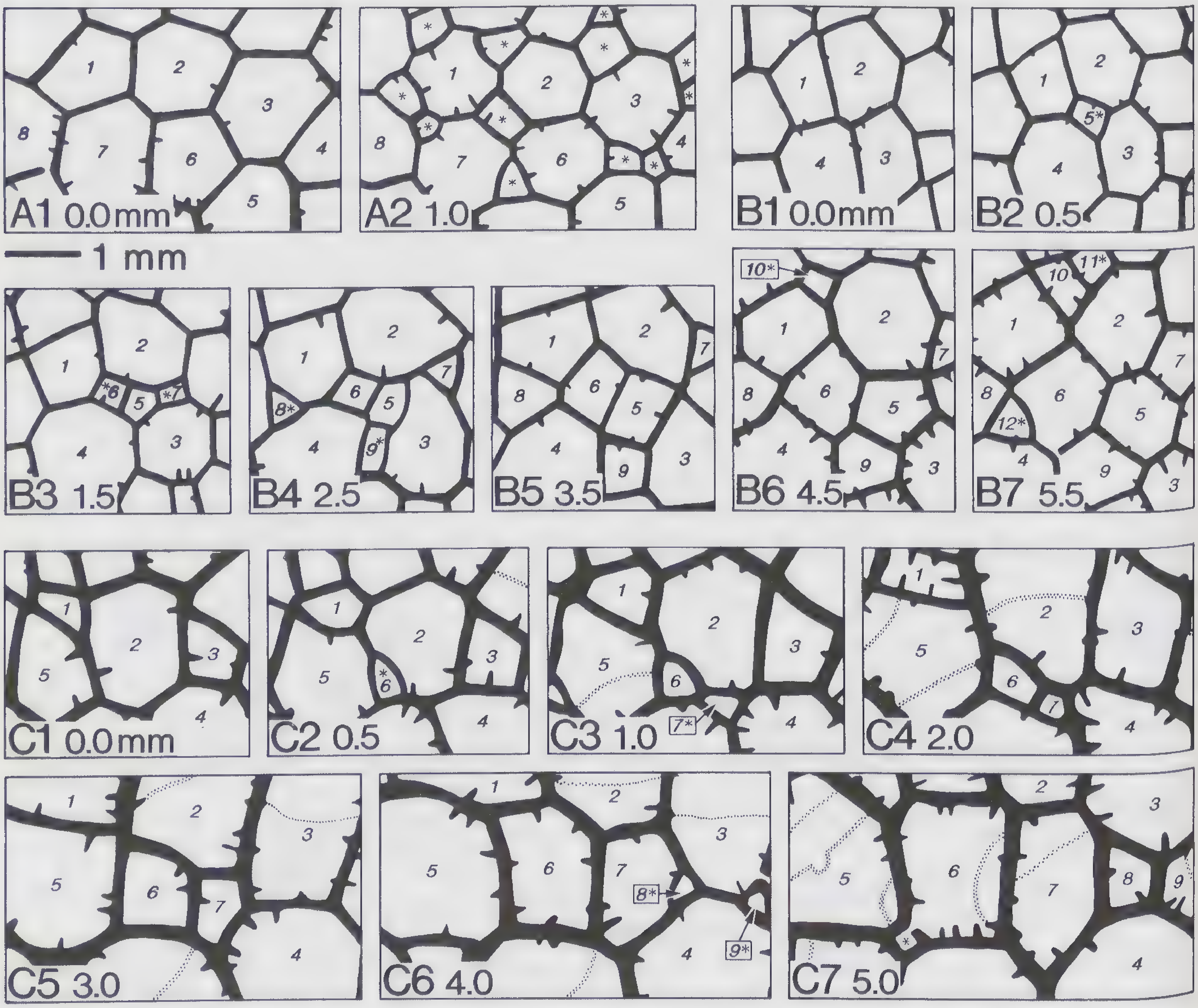
Coralla of this species are generally similar in basal character, but some significant differences appeared quite early in growth. At or near the bases of coralla, corallites tend to be small, with average dimensions commonly 0.75–1.80 mm. They are aseptate or weakly septate, of regular or somewhat variable size, and are commonly relatively thick-walled (Pl. 16, fig. 5). In coralla that went on to develop large corallites, corallum bases are broadly divergent; this is associated with a rapid increase in average corallite dimensions during the early growth stages (Pl. 16, fig. 5). In coralla of the small-corallite variant (see *Intraspecific variation*, below), bases are much less divergent, and corallites near the absolute base already have average corallite dimensions close to those seen in later stages of growth (Pl. 14, fig. 10).

During subsequent growth, corallites in the corallum axis continued to expand slowly, with corallite contraction occurring at rare intervals in some specimens.



Text-figure 22.—**A–N**, Serial transverse sections illustrating basal astogeny in a corallum of *Paleofavosites subelongus;* USNM 459086, Section-interval 16-1 (Clinton Spring) (see also Pl. 14, figs. 1–3). Corallite walls are solid, tabulae are stippled, septa are not shown; a probable algal grain is cross-hachured, a crinoid columnal is solid-hachured, sediment surrounded by the corallum is dash-hachured; scale bar is shown. Section A (0.0 mm) represents the absolute base of the corallum, heights in mm for B–N are above that datum; *P* is the protocorallite, numbers in italics represent individual hysterocorallites; an asterisk indicates the first appearance of a particular hysterocorallite.

Variability of corallite dimensions on transverse sections is commonly quite different between sections taken from different heights within a single corallum (see *Intraspecific variation,* below). Walls and septa show normal characters of development quite low in a corallum, but both tended to change through growth. Well defined cyclomorphic variation is rare (see *Description of coralla,* above); where it is present, thick-



Text-figure 23.—Serial transverse sections illustrating corallite increase in *Paleofavosites subelongus*. **A1, A2**, Burst of offsetting in a corallum where mature corallites are of regular size; USNM 459074, Section-interval 15-1 (Calumet) (see also Pl. 14, figs. 9–11). **B1-B7**, Corallite increase in a corallum having small corallites of relatively regular size; USNM 485865, Section-interval 14-1 (Higginbotham Farm). **C1-C7**, Corallite increase in a corallum having relatively large, dimetric corallites; USNM 459079, Section-interval 14-1 (Higginbotham Farm) (see also Pl. 16, figs. 1–6). Corallite walls and septa are solid, tabulae are stippled; scale bar is shown. Heights in mm are above an arbitrary datum within the mature, axial part of each corallum; numbers in italics represent individual corallites; an asterisk indicates the first appearance of a particular corallite.

ening of walls and increased density and length of septa do not always occur in conjunction with closer spacing of tabulae. Single corallites commonly extend through most or all of the height of a corallum. Skeletal elements occurring at the upper surfaces of coralla are not obviously different from those occurring below.

Corallite increase is intracalicular and peripheral (= lateral); each new corallite was produced through the development of a wall that closed off a corner or a side of the parent corallite (Text-fig. 23; Pl. 14, fig. 1, Pl. 15, fig. 11). Each offset is connected to its parent by one or two pores at or immediately above its base. New offsets have three or four sides, depending on whether the site of increase was in a corner or along a wall (Pl. 16, figs. 3, 4); sides were added as corallites grew (Young and Elias, 1993). Four-sided offsets are most common where mature corallites are more regular in size (Pl. 15, figs. 8, 12), whereas three-sided offsets predominate in coralla showing more pronounced dimetrism (Text-fig. 23; Pl. 15, fig. 11). Parent corallites were usually relatively large, typically having five to eight sides prior to offsetting. Although in many cases the parent corallite cannot be distinguished due to plane of sectioning, it seems that new offsets did not generally give rise to other offsets except during regeneration following partial mortality of the colony surface.

New corallites typically expanded quite slowly (Text-fig. 23; see *Intraspecific variation,* below). Expansion rates were highest in coralla having large adult corallites, and were significantly lower where adult corallites were smaller (Young and Elias, 1993). Each new corallite expanded into space previously occupied by the adjacent individuals (Text-fig. 23B1–B7, C1–C7). New corallites may be aseptate (Pl. 16, fig. 3) or may have very long septa (Pl. 16, fig. 11, lower right). The walls of three-sided corallites are commonly bowed outward (Pl. 14, fig. 8).

In most coralla there are obvious differences between the axis (area of vertical and subvertical growth) and the margins (areas of more lateral growth); in some coralla there is a clear distinction between these regions (Pl. 16, fig. 5). Corallites are usually straight in the axis, but they tend to be curved outward in the margins. Tabulae are more broadly spaced in the axis than in the margins; this is more marked in domical coralla than in bulbous ones. Cyclomorphic bands extend across the entire corallum. Offsetting was often concentrated in the axis, and particularly at the transition between the axis and margins. The relative width of the axis and margins reflects corallum growth patterns and the shape of the growth surface. A relatively broad axis is associated with a tall corallum having short growth surfaces. Such coralla tend to have developed where basal divergence was restricted, and where adult corallites were small. Relatively narrow axes and wider margins occur in coralla with more spreading growth forms, long growth surfaces, more basal divergence, and large corallites (see *Intraspecific variation,* below).

Sediment inclusions representing partial mortality of the colony surface occur in many specimens (Pl. 16, fig. 12). Such inclusions can occur in both marginal and axial areas. Above these inclusions, variable patterns of growth are observed. In some cases, new subvertical corallites that are slightly smaller than the previous adult individuals were initiated across the surface of a holothecal layer (Pl. 15, fig. 6). Such corallites are commonly irregular in outline and may be predominantly five-sided (Pl. 16, fig. 9); they developed normal adult size and appearance during subsequent growth. In other examples, corallites occurring lateral to an inclusion spread subhorizontally across the inclusion, giving rise to offsets before resuming subvertical growth (Pl. 16, fig. 12).

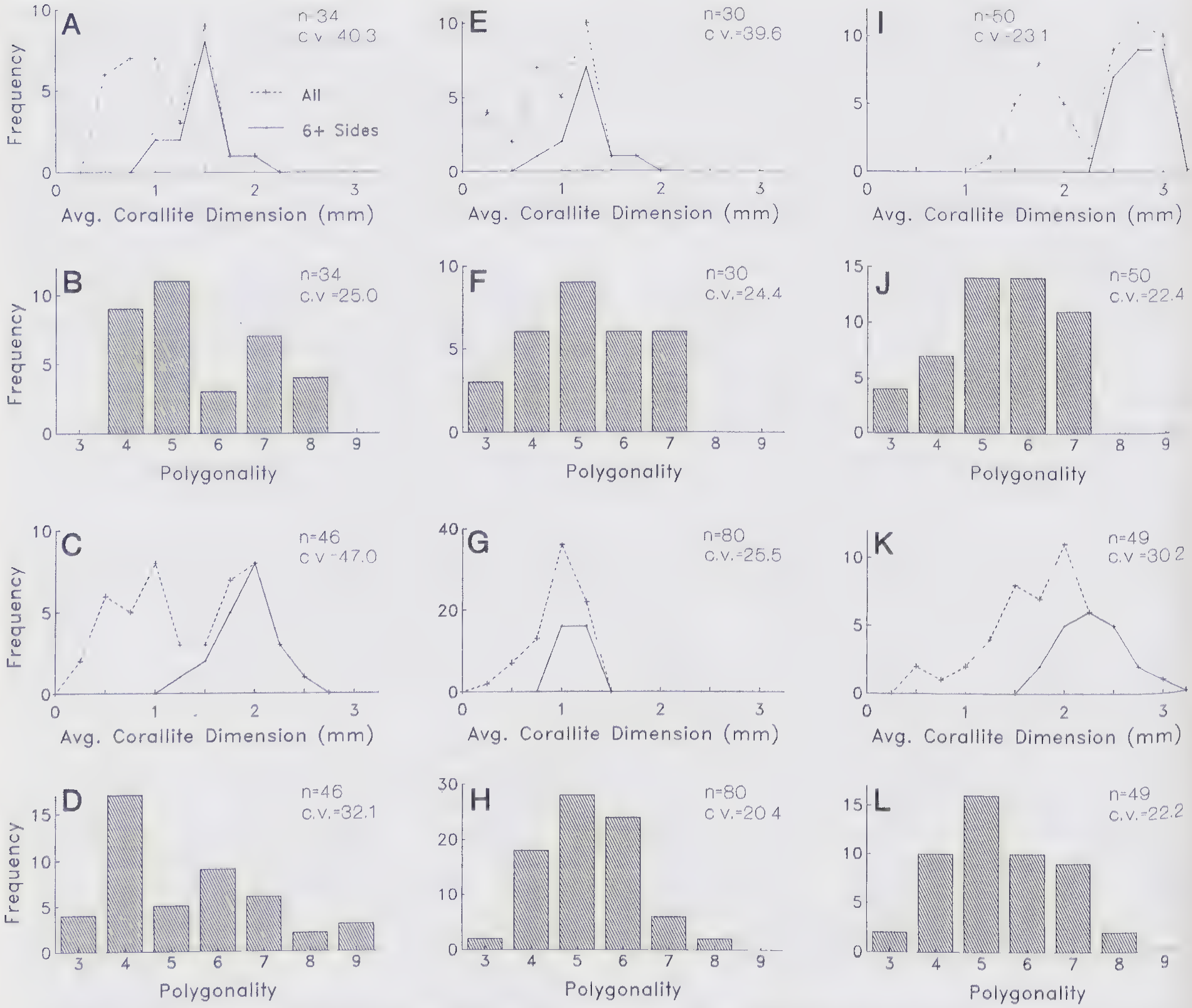
Microstructure.—The wall between any pair of corallites is composed of three layers: a "dark" median line (see Schouppé and Oekentorp, 1974, fig. 6) bounded on either side by a radially fibrous layer. The median line has a lamellar appearance. It has definite lateral boundaries and is usually slender, but its thickness varies considerably between coralla depending on preservation (Pl. 14, figs. 3, 7, Pl. 15, figs. 1, 2, Pl. 16, figs. 3, 4, 10); it can be darker or paler than the rest of the wall. The median line can maintain a consistent thickness between cyclomorphically thickened and unthickened parts of a corallum. The fibrous layers of the wall are usually buff-colored and consist of fibers that are perpendicular to the wall in transverse section, and directed upward laterally from the median line at an angle from the horizontal of about 30–60° in longitudinal section (Pl. 15, fig. 4).

Septal spines are usually embedded deep in the fibrous wall, and the fixed part of each septum follows the prevailing trend of wall fibers (Pl. 15, fig. 4). They are rarely fixed in the median line. Septa are usually denser or darker in color than the wall fibers. Most septal spines appear to be composed of bundles of subparallel fibers, rather than being truly trabecular in form. The adaxial parts of septal fibers may be straight, following the trend of the septal base (Pl. 13, fig. 7), or they may be upcurved or downcurved (Pl. 16, fig. 6).

Microstructure of tabulae is indistinct. Tabulae are embedded in the outermost margin of the fibrous wall, and are generally similar in color to that wall.

Intraspecific variation.—There is great variability among the coralla described above. This involves a number of characters, including corallite size, polygonality, wall thickness, septal development, and spacing of tabulae.

Frequency distributions of corallite size from individual transverse sections are extremely variable (Text-fig. 24A, C, E, G, I, K). Corallites added sides in a more or less regular manner as they grew, and frequency distributions of corallite size and polygonality in transverse sections tend to mimic one another (Text-fig. 24), although there are exceptions. There is no set frequency pattern of corallite size or polygonality for any one locality or corallite size range (Text-fig. 24), and distributions may vary significantly between transverse sections from different heights within a single corallum (Text-fig. 24E–H). Frequency distributions seem to have depended on periodic offsetting, and on the slow rate of corallite expansion (see *Astogeny and corallite increase,* above; *Paleofavosites subelongus,* pp. 38, 39). The modes on bimodal or polymodal distributions represent different periods of offsetting. For coralla from all localities, those corallites with six and more sides show virtually normal size distributions (Text-fig. 24A, C, E, G, I, K).



Text-figure 24.—Frequency distributions of average corallite dimension (all corallites and those with six and more sides) and polygonality for selected coralla of *Paleofavosites subelongus.* **A, B**, USNM 485822, Section-interval 31-1 (Thebes North). **C, D**, USNM 485835, Section-interval 15-1 (Calumet). **E–H**, USNM 459082, Section-interval 14-1 (Higginbotham Farm); E and F near corallum base, G and H higher in corallum. **I, J**, USNM 485855, Section-interval 14-1 (Higginbotham Farm). **K, L**, USNM 485900, Section-interval 32-1z (Thomson East). Each pair of graphs represents the same single transverse section; n = number of corallites (all), c.v. = coefficient of variation for all corallites.

Although corallite size frequency distributions are variable, there is a strong linear relationship between the average dimension of all corallites and the average dimension of corallites with six and more sides in transverse sections of this species (Text-fig. 25A). This relationship remains roughly constant with changes in corallite size. Also, the variability of corallite size within coralla does not change with changes in mean size, and there is no clear correlation within coralla between variability in size of all corallites and of those having six and more sides.

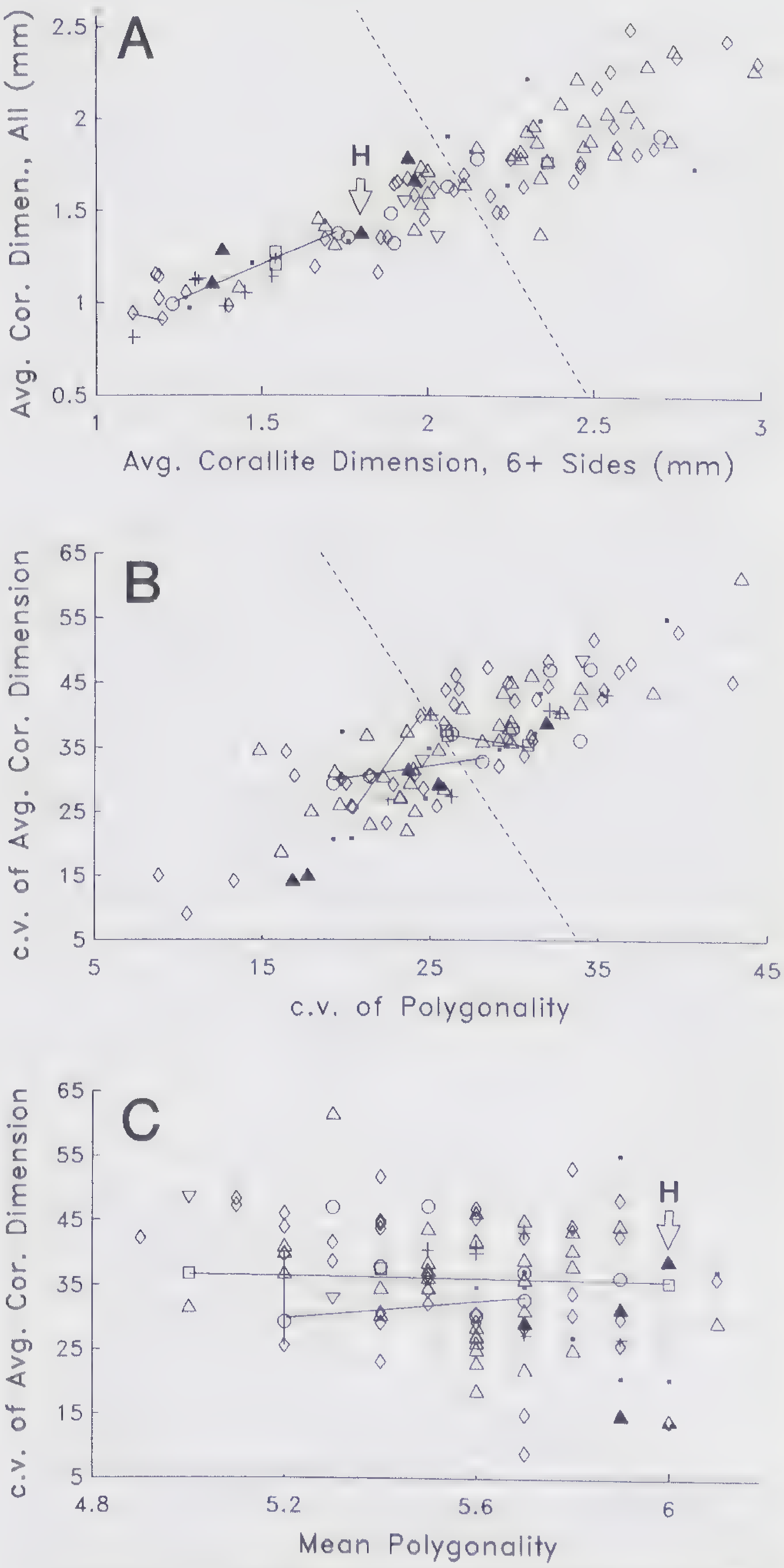
There are some differences in the range of corallite size between stratigraphic intervals for which large collections are available (Text-fig. 25A), and this variation is correlated with colony growth form. Coralla having domical forms with flat bases tend to have the largest corallites, whereas those having bulbous or columnar forms with expanding bases tend to have smaller corallites (see *Astogeny and corallite increase,* above). Coralla with the largest average corallite dimensions occur in Section-interval 32-1z (Thomson East) (mean ACD (6+) = 2.28 mm), where coralla are predominantly of high and low domical form (Table 14; Text-fig. 10). Coralla from Section-intervals 14-1 (Higginbotham

Farm) and 15-1 (Calumet) have somewhat smaller corallites (mean ACD (6+) = 2.09 mm and 1.99 mm, respectively), and coralla from these intervals are of mixed high and low domical and bulbous form (Table 14; Text-fig. 10). Coralla with much smaller corallites were collected from Section-interval 31-1 (Thebes North) (mean ACD (6+) = 1.35 mm; Text-fig. 25A). Unfortunately, data are insufficient to determine whether the coralla are predominantly tall in this collection, but it is noteworthy that the tallest forms of *Propora thebesensis* occur in the same interval.

There is a correlation between the variabilities of average corallite dimension and polygonality (Text-fig. 25B). Transverse sections having highly variable corallite sizes are also highly variable in polygonality. The variability of average corallite dimension is also correlated with the mean of polygonality (Text-fig. 25C). Where the variability of corallite size is great, the mean polygonality is often well below 6.0. This suggests that an increase in the number of three- and four-sided corallites on a surface, due to offsetting, was not quite matched by an increase in the number of corallites having seven or more sides. Most of the range of mean polygonality can occur within single coralla. Each large collection shows a considerable range of polygonality, and a range of variability in polygonality and average corallite dimension (Text-fig. 25B, C).

Comparisons between coralla in this entire collection show that a relationship exists between corallite size and the degree of development and thickening of skeletal characters. A graph of mean wall thickness *versus* average corallite dimension of adult corallites illustrates a positive correlation between these characters (Text-fig. 26A). Most localities show a broad spread of points, but there are differences; walls are generally thicker for a given corallite size in Section-interval 14-1 than in Section-interval 32-1z. Septal length also shows a positive correlation with average corallite dimension of adult corallites (Text-fig. 26B). Relatively long septa tend to occur only where adult corallites are large, but septa may also be absent in such circumstances. The diameter of corner pores has a linear relationship with average corallite dimension of mature corallites (Text-fig. 26C); data for pore diameter are not as extensive as for wall thickness or for length of septa, but there seem to be few differences between localities for this character. Wall thickness, length of septa, and pore diameter all show a positive correlation with one another, as well as being related to corallite size.

Vertical spacing of tabulae does not show any clear relationship to corallite size, but does vary with locality (Text-fig. 26D). In Section-intervals 14-1 and 15-1, spacing of tabulae is generally close but variable,

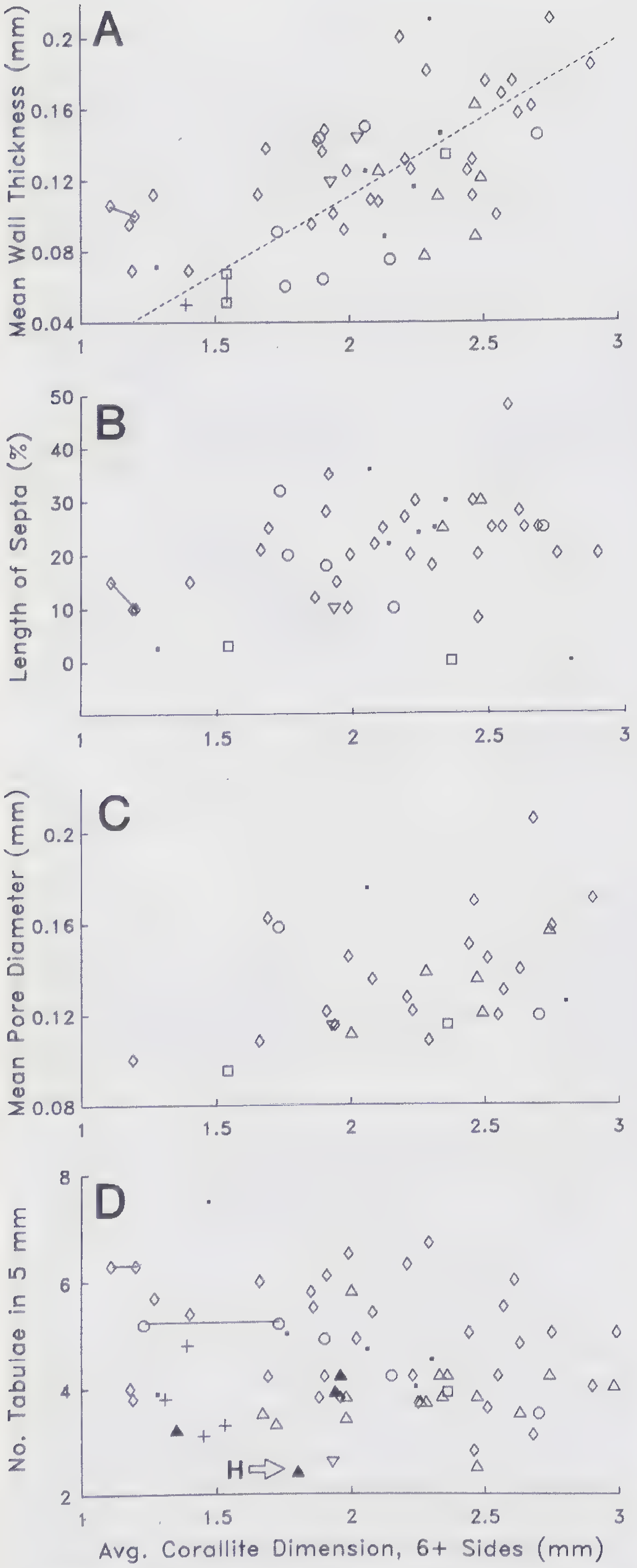


Text-figure 25.—Intercorallum variation in morphologic characters of *Paleofavosites subelongus*, Part 1. **A**, Relationship between average corallite dimension of all corallites and of those having six and more sides, for transverse sections from 102 coralla. **B**, Relationship between coefficient of variation (c.v.) of average corallite dimension (all corallites) and of polygonality for transverse sections from 102 coralla. **C**, Relationship between c.v. of average corallite dimension (all corallites) and mean polygonality for transverse sections from 102 coralla. Each data point represents a single thin section; solid lines connect sections from different parts of a single corallum; H = UI X-878a (holotype). Arbitrary dashed lines in A and B were used to derive proportions shown in part of Table 13. Symbols for Section and Section-intervals: □ 23-2 and 23-3 (Lawrence Quarry); + 31-1 (Thebes North); ▲ 5 km south of Clarksville, Missouri; ▽ 16-1 (Clinton Spring); ◇ 14-1 (Higginbotham Farm); ○ 15-1 (Calumet); △ 32-1z (Thomson East); ■ all other Section-intervals.

whereas it is broader in Section-intervals 31-1 and 32-1z, and at 5 km south of Clarksville (Table 12; Text-fig. 26D). There is no obvious general relationship between spacing of tabulae and colony growth form. Spacing of tabulae tends to be closer in marginal parts of the corallum than in the axis, and can also vary between the base and top of a corallum. This makes it difficult to compare corallum means that are in some cases based on incomplete specimens.

Discussion.—The high degree of variability observed in the collection described above makes species discrimination somewhat difficult, since such variation in several characters would be sufficient to divide the coralla into two to four species according to commonly used approaches to favositid systematics. Nevertheless, some features, such as basal morphology and the form of septa, walls, and corner pores, are reasonably consistent among all the specimens, and certain aspects of the variability in other characters support inclusion in a single species. First, a significant portion of the intercolony variation for each character may be exhibited by individual coralla. Also, corallum means for each of these characters are continuously distributed within this collection, and may show a high degree of variability within individual stratigraphic intervals. Finally, most of these characters show a moderate to strong correlation with one another; this interconnection suggests that one basic structural design was being affected by intraspecific genetic variability and environmental factors. Observations that support this interpretation are detailed under *Intraspecific variation*, above.

Savage (1913, 1917) based *Favosites subelongus* on material collected from the Cyrene Formation near Edgewood and from the Bryant Knob Formation at Louisiana and 5 km south of Clarksville, Missouri. The original description of this species emphasized corallites of variable size with dimensions up to 1.5–2.0 mm, that have corner pores and seem to lack septa. Savage's holotype (UI X-878a; Pl. 13, figs. 8, 9) and



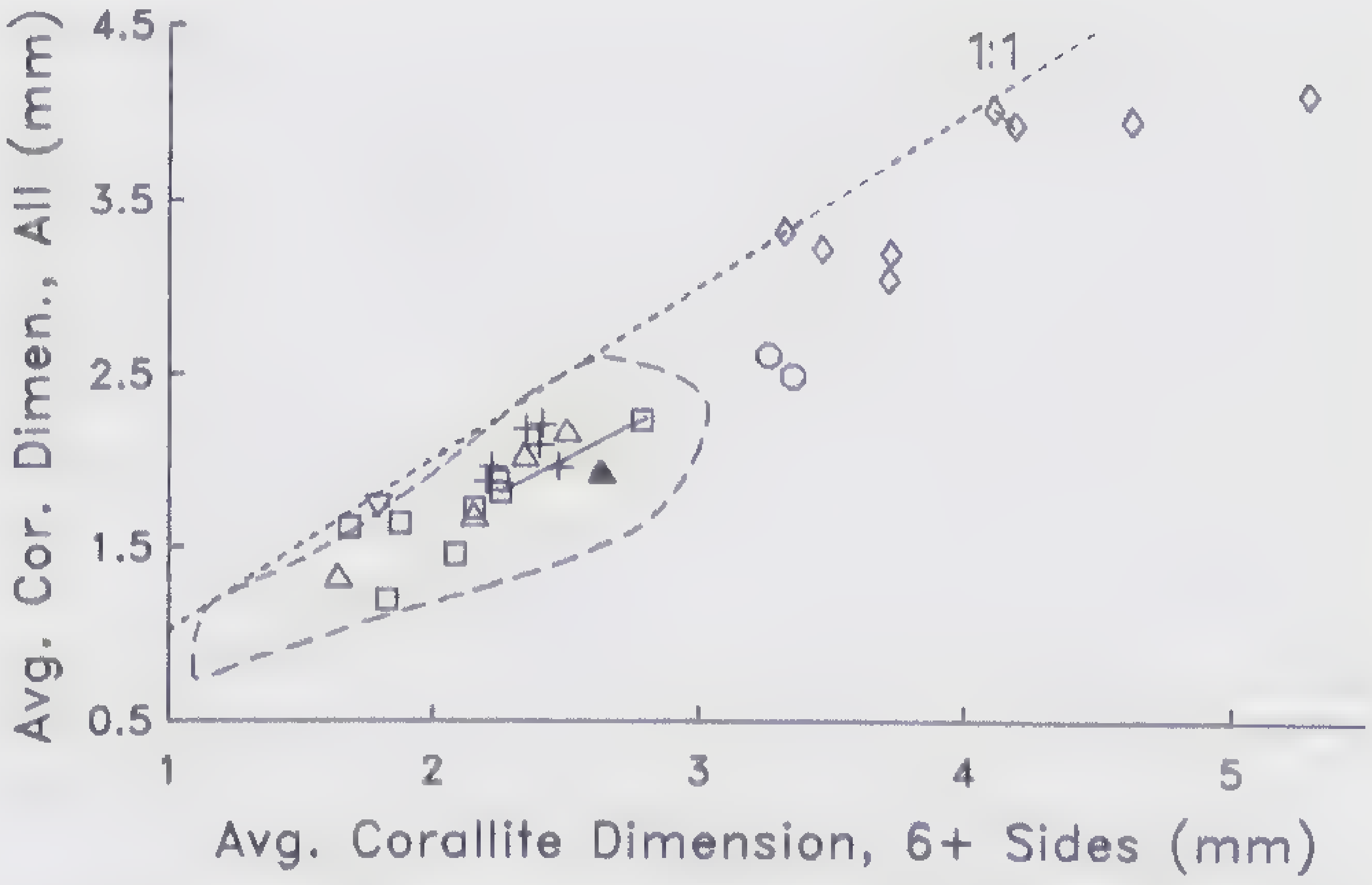
Text-figure 26.—Intercorallum variation in morphologic characters of *Paleofavosites subelongus*, Part 2. **A**, Relationship between mean wall thickness and average corallite dimension of those having six and more sides, for transverse sections from 55 coralla. **B**, Relationship between length of septa as a percentage of corallite radius and average corallite dimension of those having six and more sides, for transverse sections from 45 coralla. **C**, Relationship between mean pore diameter and average corallite dimension of those having six and more sides, for transverse sections from 31 coralla. **D**, Relationship between number of tabulae in unit 5 mm and average corallite dimension of those having six and more sides, for transverse and longitudinal sections from 67 coralla. Each data point represents a single thin section or a pair of transverse and longitudinal thin sections; solid lines connect sections from different parts of a single corallum; H = UI X-878a (holotype). Arbitrary dashed line in A was used to derive proportions shown in part of Table 13. Symbols for Section and Section-intervals are listed under Text-figure 25.

his other illustrated specimen (UI X-878b), both from 5 km south of Clarksville, are consistent with his description. Both have corallites slightly smaller than the species mean (mean ACD (6+) = 1.80 mm and 1.94 mm, respectively; compare with Table 19), short septa, thin walls, and widely spaced tabulae (Ta5 = 2.4 and 3.9, respectively). These features are consistent with those of the other material we include in *Paleofavosites subelongus,* but the holotype does not in any way represent a species "mean" for most characters.

In the same publications, Savage (1913, 1917) erected *Calapoecia favositoidea.* This species was listed as occurring at exactly the same localities as *F. subelongus,* and was described as having polygonal corallites with dimensions of 1.5–2.5 mm, in contact, and walls with spiniform ridges. Savage's diagram of a transverse section and photograph of *C. favositoidea* (Savage, 1913, pl. 3, figs. 1, 3; 1917, pl. 5, figs. 1, 3) show characters that are completely consistent with those of *Paleofavosites subelongus,* and the two species are considered to be synonyms. Savage's assignment of *C. favositoidea* to *Calapoecia* was apparently based on his interpretation of corallite walls exposed in longitudinal section as areas of small pores (see Savage, 1913, pl. 3, fig. 2; 1917, pl. 5, fig. 2). The specimen labelled as the holotype of *C. favositoidea* (UI X-771; Pl. 14, figs. 4–6) is not the same as that illustrated by Savage (1913, pl. 3, fig. 1; 1917, pl. 5, fig. 1); the original specimen is apparently lost. All identifiable specimens collected by Savage that are labelled as *C. favositoidea* (UI X-771, C-1457, C-1458b–g, and C-1465a, b) are members of *P. subelongus* (see also Pl. 13, figs. 10, 11, Pl. 15, figs. 1, 2).

Among the other described species of *Paleofavosites, P. subelongus* is most similar to *Paleofavosites* sp. cf. *P. forbesiformis* from the lower part of member 1 of the Becscie Formation on Anticosti Island, Québec (lowermost Silurian, Lower Llandovery, lowermost Rhuddanian; Melchin *et al.,* 1991, p. 1861), as illustrated by Bolton (1981a; unit referred to as member 6 of the Ellis Bay Formation therein). We examined the following specimens, collected by T. E. Bolton in 1957 and 1958: GSC 66830 (Bolton, 1981a, pl. 2, fig. 3), 66831 (Bolton, 1981a, pl. 2, fig. 4), 66839 (Bolton, 1981a, pl. 3, fig. 9), and 66840 (Bolton, 1981a, pl. 3, fig. 10).

Bolton's specimens of *Paleofavosites* sp. cf. *P. forbesiformis* are similar to *P. subelongus* for most characters, including corallite size, wall thickness, and form of pores and septa (biometric data for the Anticosti *Paleofavosites* sp. cf. *P. forbesiformis:* ACD (all) = 1.32–2.16 mm, ACD (6+) = 1.64–2.50 mm, CoA = 1.59–4.35 mm^2, Pol = 5.8–6.0, WT = 0.100–0.129 mm, LS = 4–22%, PoD = 0.114–0.130 mm, Ta5 = 5.6–6.1; compare with Table 19; see Text-fig. 27). They differ from *P. subelongus* by having wavier walls and more crenulate tabulae, and one specimen (GSC 66830) appears to have more abundant mid-wall pores than does *P. subelongus.* These species are questionably synonymized here.



Text-figure 27.—Comparison of selected species of *Paleofavosites:* relationship between average corallite dimension of all corallites and of those having six and more sides, on transverse sections. Each data point represents a single thin section; solid line connects sections from different parts of a single corallum. The short-dashed line is for a relationship of 1:1; any point along this line represents a section on which all corallites are as large as those having six and more sides. A long-dashed line surrounds the field of distribution for 102 coralla of *P. subelongus* from the east-central United States. Symbols for other species: □ *Paleofavosites* sp. cf. *P. subelongus;* east-central United States; n (number of coralla) = 7; ◇ *P. adaensis;* east-central United States; n = 7; ○ *Paleofavosites* sp. cf. *P. ivanovi;* east-central United States; n = 2; + *Paleofavosites* sp. A; east-central United States; n = 6; △ *Paleofavosites* sp. cf. *P. forbesiformis;* Becscie Formation, Anticosti Island, Québec; n = 4; ▲ *P. capax;* Gun River Formation, Anticosti Island, Québec; n = 1; ▽ *P. prolificus;* Chasm Creek Formation, northern Manitoba; n = 1.

Palaeofavosites [*sic*] *forbesiformis* was originally described and illustrated by Sokolov (1951b) from the Juuru Stage of Estonia (Rhuddanian), and was documented under the same name from erratic boulders in Poland by Stasinska (1967). Their specimens have corallites with dimensions of 0.5–2.4 mm and 0.6–2.0 mm, respectively; because they have very thin walls and lack septa, and because Stasinska's (1967, pl. 16, fig. 1a) photograph of a transverse section seems to show some mid-wall pores, they are listed with a *confer* in our synonymy.

The names *Paleofavosites prolificus* and *Paleofavosites capax,* both erected for species originally described from Anticosti Island, have been used by several authors for corals having characters similar to those of *P. subelongus.* Billings (1865, p. 429) proposed *Favosites prolificus* to include specimens from the Vauréal Formation (Hudson River Group of Billings: Upper

Ordovician, Richmondian; Petryk, 1981, fig. 4) and from higher parts of the Anticosti sequence. His description of *F. prolificus* includes corallite diameters of about 2 mm ("about 1 line" in Billings), numerous tabulae, and no identifiable septa or mid-wall pores (on hand specimens). The following year, Billings (1866, p. 6) republished the same description. On the same page, he erected *Favosites capax* to include corals from the "West end" of Anticosti Island (Vauréal Formation?) having corallites with diameters of about 4 mm ("about 2 lines" in Billings) with a few smaller individuals between them, thin and flat tabulae, and corner pores. Both of these original descriptions are sufficiently general that they could refer to several different taxa. Unfortunately, the type material of both species has been lost (Bolton, written commun., 1991), and both *P. prolificus* and *P. capax* require extensive re-assessment. This uncertain status makes comparisons difficult.

Later works dealing with corals from several formations on Anticosti Island have used the species names *prolificus* and *capax*. These include studies by Twenhofel (1914, p. 24; 1928, pp. 125–127), Bolton (1981a, pl. 1, fig. 8, pl. 9, fig. 10), and Lee and Noble (1990, pp. 257–272, figs. 1–14, tables 1, 2). None, however, has described or illustrated these species in sufficient detail to permit satisfactory comparisons. From the available information, it is probable that some of the Anticosti specimens referred to *P. prolificus* are very similar to *P. subelongus*. Also similar is a specimen of *P. capax* from the lower part of member 5 of the Ellis Bay Formation (uppermost Ordovician, Gamachian; Petryk, 1981, fig. 4), illustrated by Bolton (1981a, pl. 1, fig. 8; member 5 therein). It has short septa and crenulate tabulae, but its corallites with adult dimensions of 3.2–4.0 mm are somewhat larger than those of *P. subelongus*. Other material is quite different; specimens of *P. capax* illustrated by Bolton (1980, pl. 2.7, fig. 4) from the Ellis Bay Formation and by Bolton (1981a, pl. 9, fig. 10) from the Gun River Formation (Middle Llandovery, lower Aeronian; Barnes, 1988, fig. 2) have large corallites, thin walls that have some mid-wall pores, and very rare short septa (see *Discussion* under *Paleofavosites* sp. cf. *P. ivanovi*, p. 95, for biometric data on the Gun River specimen). Bolton's (1980, pp. 22, 25, pl. 2.7, figs. 1, 5, 6) *P. capax* from the Burmingham Member of the White Head Formation near Percé, Québec (Upper Ordovician, Ashgill, pre-Hirnantian; see Skidmore and Lespérance, 1981, p. 38; Lespérance *et al.*, 1987, fig. 4), has large corallites with adult dimensions of 3.3–4.0 mm, thin walls, and some mid-wall pores.

Corals from other parts of North America have been described as *P. prolificus* and *P. capax* by several authors. Like the Anticosti Island material, all of them require detailed re-study. Corals referred to *P. prolificus* are generally the most similar to *P. subelongus*. Stearn (1956, p. 60, pl. 4, fig. 1, pl. 10, fig. 13) described and illustrated as *P. prolificus* corals from the Stony Mountain Formation (Upper Ordovician, Richmondian; Sweet, 1979, fig. 4), Stonewall Formation (uppermost Ordovician–Rhuddanian; Sweet, 1979, p. 54, fig. 4; Johnson and Lescinsky, 1986, fig. 2), Inwood Formation (Aeronian; Johnson and Lescinsky, 1986, fig. 2), and East Arm Formation (Upper Llandovery, Telychian; Johnson and Lescinsky, 1986, fig. 2) of southern Manitoba. These are described as having corallites with uniform dimensions of about 2.3 mm, corner pores, rare mid-wall pores, and short septal spines; Stearn's illustrations show coralla that seem to have much more densely spaced tabulae and more abundant mid-wall pores than does *P. subelongus*. Stearn (1956, p. 61, pl. 10, fig. 12) also described *P. capax* from the upper members of the Stony Mountain Formation and from the Stonewall Formation. This has much larger corallites with adult dimensions of about 3.8 mm, very thin walls, and rare or absent septa.

Nelson (1963) described *Palaeofavosites* [*sic*] *prolificus* from members 1 and 2 of the Chasm Creek Formation, Hudson Bay Lowland, northern Manitoba (Richmondian; see Elias, 1991, fig. 3). We examined Nelson's illustrated specimen, which he collected in 1950 (GSC 10329); it is very similar to *P. subelongus*, having moderately thin-walled, regular-sized corallites that appear to lack septa and have corner pores only (biometric data: ACD (all) = 1.74 mm, ACD (6+) = 1.79 mm, CoA = 2.74 mm^2; see Text-fig. 27). It is listed with a *confer* in our synonymy. Nelson (1963, pp. 52–53, pl. 7, fig. 4) also documented *Palaeofavosites* [*sic*] *capax* from member 1 and the upper member of the Caution Creek Formation and from the Chasm Creek Formation, Hudson Bay Lowland, northern Manitoba (all Richmondian; see Elias, 1991, fig. 3). This species is very different, having very large mature corallites with dimensions of about 4–5 mm.

Paleofavosites sp. cf. *P. capax* was described but not illustrated by Pandolfi (1985, pp. 28, 29) from the Upper Ordovician Lost Canyon and Floride members of the Ely Springs Dolomite of Nevada and Utah. This material is distinguished from *P. subelongus* by its larger corallites with dimensions of 1.5–4.2 mm.

Laub (1979, pp. 263–271, pl. 9, figs. 1–5, pl. 29, figs. 3, 4, pl. 39, figs. 1, 3) described a *P. prolificus* from the mid-Llandovery Brassfield Formation of Ohio and possibly of Indiana and Kentucky. This species is not very similar to *P. subelongus*. It has corallites of regular size with dimensions of about 1.0–1.5 mm and, according to the description, possesses corner pores only.

One illustration (Laub, 1979, pl. 29, fig. 4), however, shows common mid-wall pores in some parts of a corallum.

Another species similar to *P. subelongus* is *Paleofavosites nodosus* Poulsen (1941, p. 22, pl. 4, figs. 4–6), from the Offley Island Formation of north Greenland (Upper Llandovery). The latter species has corallites of variable size, the larger ones with dimensions of about 2.0–2.5 mm, and has corner pores only. The illustrations are not sufficiently clear for more detailed comparisons.

Among the other species occurring in the uppermost Ordovician and lowermost Silurian of the east-central United States, *P. subelongus* shares some characters with *Paleofavosites* sp. cf. *P. subelongus, Paleofavosites* sp. cf. *P. ivanovi,* and *Paleofavosites* sp. A. Comparisons are included in the *Discussion* under each of those species.

Occurrences.—Uppermost Ordovician (Gamachian): lower Keel Formation, south-central Oklahoma; Leemon Formation, southern Illinois. Uppermost Ordovician (Gamachian) to lowermost Silurian (?; Lower Llandovery?, lower Rhuddanian?): Cyrene Formation, northeastern Missouri. Uppermost Ordovician (?; Gamachian?) to lowermost Silurian (Lower Llandovery, lower Rhuddanian): Wilhelmi Formation, northeastern Illinois; lower Mosalem Formation, northwestern Illinois. Lowermost Silurian (?; Lower Llandovery?, lower Rhuddanian?): unnamed member and Kissenger Limestone Member, Bryant Knob Formation, northeastern Missouri.

Possibly in lowermost Silurian (Lower Llandovery, lowermost Rhuddanian): lower part of member 1, Becscie Formation, Anticosti Island, Québec.

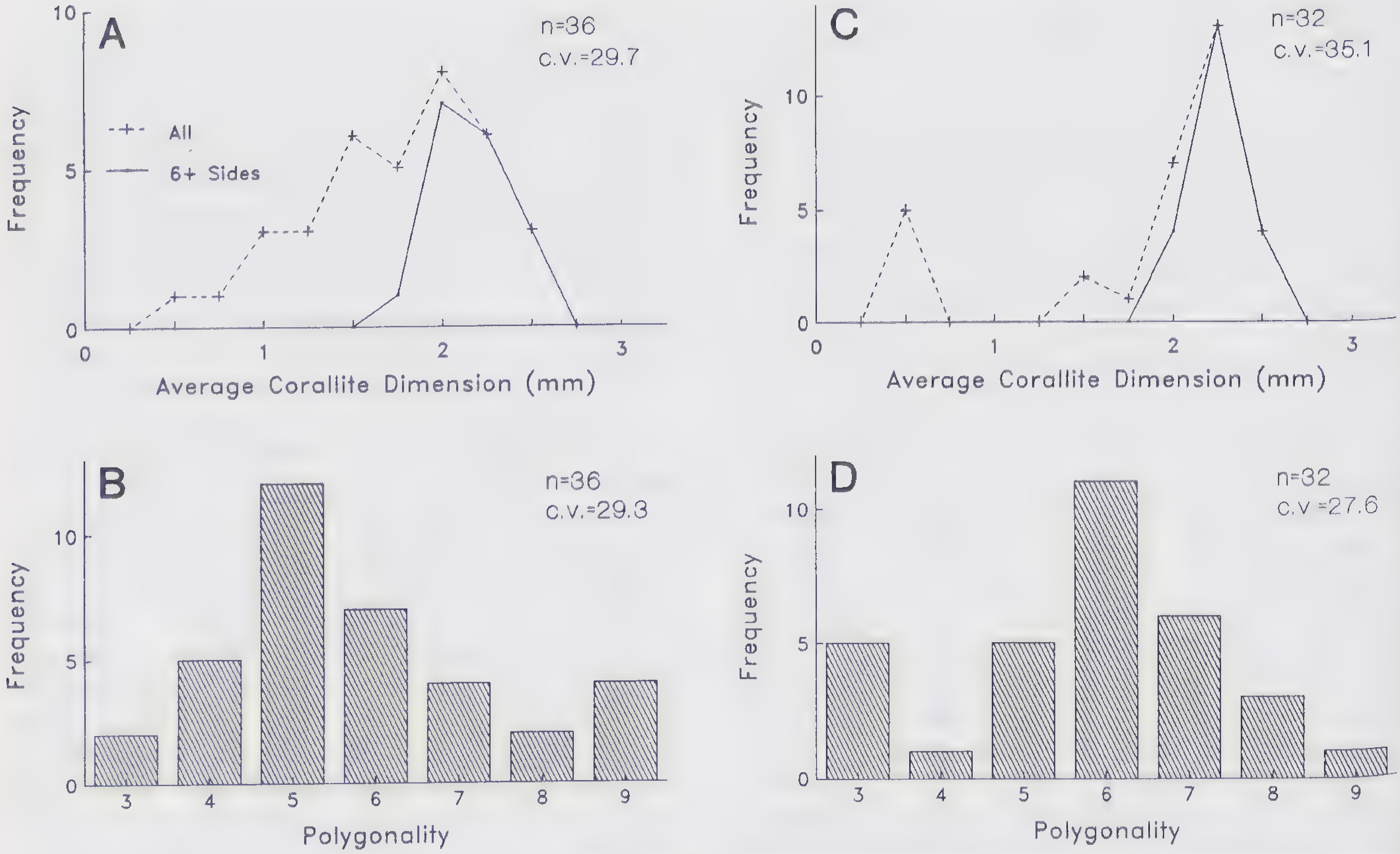
Holotype.—UI X-878a (Savage, 1913, pl. 3, fig. 10; Savage, 1917, pl. 5, fig. 10; Pl. 13, figs. 8, 9), collected by T. E. Savage (labelled "*Favosites subelongus,* Silurian, Edgewood [Formation], 3 mi. S. of Clarksville, Mo."), Bryant Knob Formation, 5 km south of Clarksville, Pike County, Missouri.

Other material described above.—144 specimens: USNM 485785a, site 23iv, interval 23-2 (*Brevilamnulella* beds), USNM 458776, 485816, site 23i, interval 23-3, Keel Formation, Section 23 (Lawrence Quarry), Pontotoc County, Oklahoma; USNM 485817, interval 21-1b, Ideal Quarry Member, Keel Formation, Section 21 (Rock Crossing), Carter County, Oklahoma; USNM 485818–485823, interval 31-1, Leemon Formation, Section 31 (Thebes North), Alexander County, Illinois; USNM 485824–485826, interval 18-1, unnamed member, USNM 485827, interval 18-2, Kissenger Limestone Member, Bryant Knob Formation, Section 18 (Kissenger), Pike County, Missouri; UI X-878b, C-1466a, collected by T. E. Savage (labelled "*Favosites subelongus,* Edgewood [Formation], 3 mi. S. of Clarksville, Mo."), UI C-1462b, collected by T. E. Savage (labelled "*Lyellia thebesensis,* Edgewood [Formation], 3 mi. S. Clarksville, Mo."), UI C-1465a, C-1465b, collected by T. E. Savage (labelled "*Calapoecia favositoidea,* Edgewood [Formation], 3 mi. S. Clarksville, Mo."), Bryant Knob Formation, 5 km south of Clarksville, Pike County, Missouri; USNM 459086, 485828, interval 16-1, Kissenger Limestone Member, Bryant Knob Formation, Section 16 (Clinton Spring), Pike County, Missouri; UI X-771, collected by T. E. Savage (labelled "*Calopoecia* [*sic*] *favositoidea,* Edgewood [Formation], Louisiana"), Bryant Knob Formation, Louisiana, Pike County, Missouri; USNM 459074, 485829–485835, 485836a–c, interval 15-1, Kissenger Limestone Member, Bryant Knob Formation, Section 15 (Calumet), Pike County, Missouri; USNM 459078, 459079–459081, 459082, 485812a, 485837–485856, 485857a, 485857b, 485858a–d, 485859–485873, interval 14-1, Kissenger Limestone Member, Bryant Knob Formation, Section 14 (Higginbotham Farm), Pike County, Missouri; USNM 485874, 485875, interval 13-0, Cyrene Formation, Section 13 (Bowling Green), Pike County, Missouri; UI C-1457, collected by T. E. Savage (labelled "*Calapoecia favositoidea,* Edgewood [Formation], near Edgewood, Mo."), UI C-1458b–g, collected by T. E. Savage (labelled "*Calapoecia favositoidea,* Edgewood Ls., near Edgewood, Mo."), Cyrene Formation, near Edgewood, Pike County, Missouri; USNM 485876, 485877, interval 37-1, Wilhelmi Formation, Section 37 (Essex), Kankakee County, Illinois; UI C-162a, C-162b, collected by T. E. Savage (labelled "*Favosites subelongus,* Edgewood ls., [locality] A-1C"), UI C-1592, collected by T. E. Savage (labelled "*Favosites subelongus,* 1 mi. below Channahon ls. otc."), Wilhelmi Formation, 3.2 km south of Channahon, Will County, Illinois; USNM 485878, 485879, 485880a, 485880b, 485881–485926, interval 32-1z, Mosalem Formation, Section 32 (Thomson East), Carroll County, Illinois.

Paleofavosites species cf. **P. subelongus**
(Savage, 1913)
Plate 17, figures 8–12

Description.—Coralla have low domical and low and high bulbous growth forms (Table 14). Size range is 31–43 mm wide and 20 to more than 30 mm high.

In transverse section, corallites appear as polygons of regular or slightly irregular shape (Pl. 17, figs. 9, 11). Average corallite dimensions are variable, 0.4–3.0 mm; average dimensions of adult corallites are commonly 1.5—2.6 mm (Table 19). Mean corallite areas on transverse sections are about 2–4 mm^2 (Table 19). New corallites have three or four sides; sides were added



Text-figure 28.—Frequency distributions of average corallite dimension (all corallites and those with six and more sides) and polygonality for two coralla of *Paleofavosites* sp. cf. *P. subelongus*. **A**, **B**, USNM 485930, **C**, **D**, USNM 485932, both from Section-interval 32-1c (Thomson East). Each pair of graphs represents the same single transverse section; n = number of corallites (all), c.v. = coefficient of variation for all corallites.

with growth, and mature individuals commonly have up to eight or nine sides, rarely up to 12 sides (Table 19). On most transverse sections, a considerable degree of variability of corallite shapes and sizes occurs (Pl. 17, figs. 9, 11; see *Intraspecific variation,* below). In longitudinal section, corallites are straight, or may be gently curved away from the colony axis.

Corallite walls are straight or broadly curved (Pl. 17, fig. 9). Walls appear to be thin to moderately thick, but thickness and structure could not be accurately determined due to poor preservation. Corner pores and mid-wall pores are both rare to common (Pl. 17, figs. 8, 11). Corner pores are simple, with diameters of 0.1–0.2 mm (Table 19). The end of a wall adjacent to a corner pore is often square and bulges slightly. Mid-wall pores have diameters of about 0.1–0.2 mm.

In transverse section, septa are short (Pl. 17, fig. 9) to moderately long and thorn-like, or absent (Pl. 17, fig. 11). They are slightly upturned adaxially, and often have thickened bases. Tabulae are thin; flat, wavy, or slightly convex or concave (Pl. 17, figs. 10, 12). They are usually complete, rarely incomplete. Tabulae are often quite broadly spaced, averaging about five in 5 mm (Table 19); in some coralla, tabular spacing shows marked periodicity, with distinct horizontal bands having much denser spacing of tabulae.

Intraspecific variation.—This collection shows quite a high degree of variability in corallite size and polygonality. Corallite size-frequency distributions on transverse sections show one or more modes (Text-fig. 28A, C). For coralla having bimodal or polymodal distributions, adult corallites with six and more sides show a virtually normal distribution under the largest mode. In one corallum, the frequency distribution for polygonality roughly parallels that for corallite dimensions (Text-fig. 28C, D). Such a relationship is not apparent in another specimen because the size mode representing adult individuals is spread more evenly among corallites having six to nine sides (Text-fig. 28A, B).

Average corallite dimensions for all corallites and for those corallites with six and more sides on transverse sections show a positive correlation (Text-fig. 27, *Paleofavosites* sp. cf. *P. subelongus*). There is a considerable degree of variation in these characters among the seven measured coralla; the most disparate transverse section is from a corallum for which a second section plots close to those for the other coralla.

Discussion.—The coralla described above are similar to the older *Paleofavosites subelongus* (latest Ordovician–earliest Silurian) in all characters except mid-wall pores, which are rare in *P. subelongus* but are common in this collection. For that reason, and because of poor preservation, these specimens are identified as *Paleofavosites* sp. cf. *P. subelongus.* They are especially similar to the coralla of *P. subelongus* occurring lower in the Mosalem Formation at the same locality, Section 32 (Thomson East) (Pl. 17, figs. 4–7; see Text-figs. 25A, 27). As described elsewhere (see *P. subelongus,* p. 40), mid-wall pores have not been seen in definitely Ordovician members of *P. subelongus,* but appear in the earliest Silurian. The increased abundance of this character through time seems to represent a phyletic trend, and *Paleofavosites* sp. cf. *P. subelongus* probably evolved from *P. subelongus.*

See the *Discussion* under *P. subelongus* (pp. 87–89) for comparisons with other species.

Occurrence.—Lower Lower Silurian (Lower Llandovery, upper Rhuddanian): upper Mosalem Formation, northwestern Illinois.

Material described above.—Nine specimens: USNM 485927–485935, interval 32-1c, Mosalem Formation, Section 32 (Thomson East), Carroll County, Illinois.

Paleofavosites adaensis, new species
Plate 18, figures 1–11

Derivation of name.—This species is named for the town of Ada, Oklahoma, which is 12 km north-northeast of the type locality.

Diagnosis.—*Paleofavosites* with large corallites, adult average corallite dimensions commonly 3.2–5.5 mm; corallite sizes and shapes often regular. Walls thin. Corner pores and mid-wall pores both rare to common. Septa absent or consisting of rare, short spines. Tabulae often crenulate, of variable form, complete or incomplete. Coralla commonly have basal holothecae.

Description of coralla.—Two measured coralla are tabular (Table 14), 45–125 mm wide and 7–20 mm high. Other coralla are broken, but appear to have had low domical and bulbous growth forms.

In transverse section, corallites are polygonal, often of regular size (Pl. 18, fig. 5). Average corallite dimensions are 0.6–5.8 mm; average dimensions of adult corallites are commonly 3.2–5.5 mm (Table 19). Mean corallite areas on transverse sections are about 8–17 mm^2 (Table 19). Corallites have three to 10 sides (Table 19). Distribution of corallite shapes depends on variability of average corallite dimensions; in most transverse sections, the majority of corallites have regular sizes and have five to seven sides (Pl. 18, fig. 5); in other sections, large corallites with eight or nine sides are interspersed in places with small individuals having three or four sides (Pl. 18, fig. 9; see *Intraspecific variation,* below). In longitudinal section, corallites are straight or gently curved, occasionally geniculate.

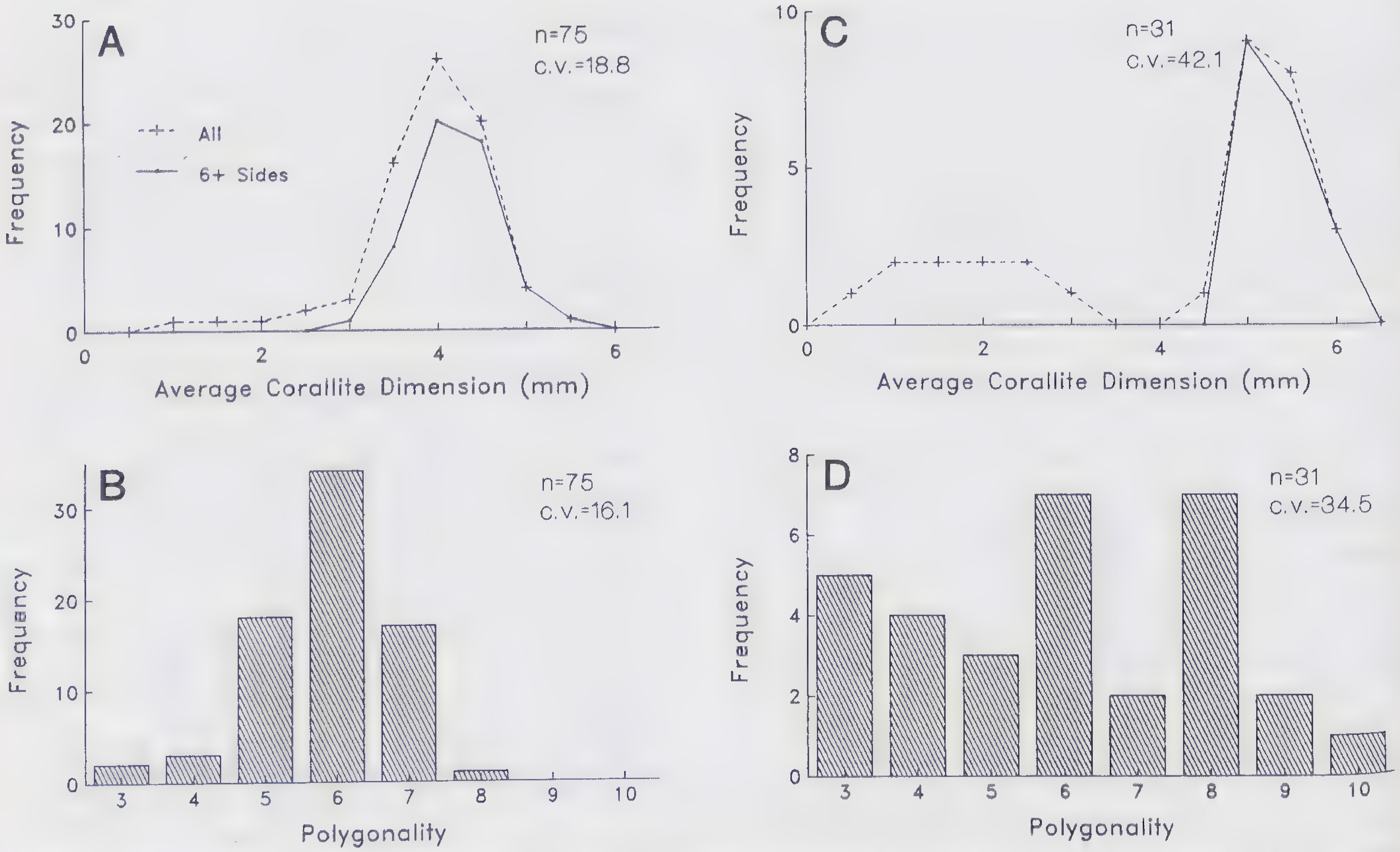
Corallite walls are straight, slightly curved, or wavy in transverse section (Pl. 18, fig. 5). Walls are usually thin, but thickness is variable, commonly 0.025–0.075 mm (Table 19). In longitudinal section, walls are wavy (Pl. 18, figs. 4, 10). Corner pores and mid-wall pores are both rare to common. Corner pores are simple, commonly with diameters of 0.1–0.3 mm (Table 19). In some cases the free end of the wall adjacent to a corner pore is rounded (Pl. 18, fig. 8). Mid-wall pores are arranged in one or two vertical rows per wall; diameters are about 0.15–0.30 mm. The end of a wall adjacent to a mid-wall pore may be slightly rounded (Pl. 18, fig. 7) or square. Septa are generally absent; short spinose septa occur rarely in some coralla (Pl. 18, fig. 3).

Tabulae are thin, crenulate, slightly convex, concave, or irregular, and complete or incomplete (Pl. 18, figs. 3, 4, 10). Tabulae often have abaxial upward deflections near the wall. Tabular spacing varies among localities; spacing may be very close or quite broad, averaging about five tabulae in 5 mm (Table 19). Tabulae may appear as partial or complete rings in transverse section, or their crenulate margins may appear as a series of arcuate lines.

Astogeny and corallite increase.—Descriptions are based largely on a single serial-sectioned corallum (USNM 485937). Other specimens are used for comparison.

The absolute base of the serial-sectioned corallum is unknown. In other specimens, corallites may extend upward from broad basal holothecae, or there may be a small group of corallites that apparently grew from a single point prior to the expansion of a basal holotheca (Pl. 18, figs. 2, 3). In some cases the basal holotheca has short spines on its upper surface (Pl. 18, fig. 2). Corallites are large and regular in the lowest known parts of the serial-sectioned corallum (see *Intraspecific variation,* below). During subsequent growth, cyclomorphic variation is represented mostly by changes in spacing of tabulae (Pl. 18, figs. 4, 10); there is little variation in thickening of skeletal elements with height in a corallum. In most specimens, some corallites extend through most or all of the height of a corallum. Dense tabular spacing occurs at the uppermost surfaces of some coralla.

Corallite increase is intracalicular and peripheral. Offsets are generally rare in mature parts of each cor-



Text-figure 29.—Frequency distributions of average corallite dimension (all corallites and those with six and more sides) and polygonality for two coralla of *Paleofavosites adaensis*. **A, B,** USNM 485937 (paratype), Section-interval 35-1 (Henry House Falls). **C, D,** UI C-1351, Alexander County, Illinois. Each pair of graphs represents the same single transverse section; n = number of corallites (all), c.v. = coefficient of variation for all corallites.

allum, but may be locally common. Most new offsets have four sides, and each was initiated along one wall of the parent corallite. Three-sided offsets are rarer; each was initiated in a corner of the parent corallite. Groups of offsets occur where a colony regenerated following partial mortality. Such offsets can have four or five sides; walls that are not in contact with other corallites are curved (Pl. 18, fig. 6). All offsets added sides as they grew.

Coralla show some lateral spreading, but much growth was regular and vertical. Offsetting is concentrated at the absolute corallum margins, and in zones of regeneration following partial colony mortality (Pl. 18, fig. 6); in both locations, considerable areas tend to be covered by offsets only. Zones of partial mortality are often represented by sediment inclusions within the corallum (Pl. 18, fig. 4); regeneration was accomplished through the expansion of a holotheca across a sediment inclusion, with new corallites being initiated across the upper surface of the holotheca. Bands of very dense tabular spacing often occur immediately below and adjacent to sediment inclusions (Pl. 18, fig. 4). Since much corallum growth was vertical, there is little character variation between the axis and margins.

Microstructure.—The wall between each pair of corallites is composed of three layers: a dark median line bounded on either side by a paler radially fibrous layer (Pl. 18, figs. 5, 7, 8). The median line appears to have a lamellar microstructure and has definite lateral boundaries. It is usually slender, but may thicken slightly at wall junctions. The fibrous wall layers consist of fibers that are perpendicular to the wall in transverse section, and are perpendicular or directed upward laterally from the median line at angles of up to 30° in longitudinal section.

The holotheca consists of an inner fibrous layer and a darker, apparently lamellar outer (basal) layer (Pl. 18, fig. 2). Fibers in the fibrous layer are oriented approximately perpendicular to the holotheca. In one corallum, short fibrous spines project upward from the fibrous layer (Pl. 18, fig. 2). The darker outer layer is about the same thickness as the dark median line in a corallite wall, and has a similar texture and appearance to that of the dark line.

Microstructure of tabulae is indistinct. Lateral margins of tabulae are embedded in the outer fibrous wall.

Intraspecific variation.—Analysis of variation was limited by the small number of specimens available.

There is little variation between coralla or between localities in several characters, including septal development, wall thickness, and form of pores. Other characters, such as corallite size and spacing of tabulae, are obviously different between localities (see below).

In general, frequency distributions for transverse sections above the basal part of each corallum show a predominance of adult corallites (Text-fig. 29A, C). This reflects the concentration of most offsetting at or near the base of each corallum. The slight differences in distribution of average corallite dimensions between the two coralla in Text-figure 29 reflect variations in growth pattern. Virtually all offsetting in a tabular corallum (Text-fig. 29A) was basal, but in a corallum that apparently had a bulbous form later offsetting also occurred (Text-fig. 29C). Distributions of corallite polygonality (Text-fig. 29B, D) parallel those for average corallite dimension, reflecting the addition of sides to corallites as they expanded. There is also a positive correlation between the average dimension of all corallites and the corallite dimension of those having six or more sides on the same transverse section (Text-fig. 27).

Variation in these and some other characters is distinctly related to locality. Specimens from Section-interval 23-5 (Lawrence Quarry) are similar to those from the Sexton Creek Limestone in southern Illinois (UI C-1347, C-1351). Coralla from both collections show somewhat variable corallite size distributions in conjunction with widely spaced tabulae (see Pl. 18, figs. 1, 3, 9, 10); growth forms are bulbous or domical. Coralla from Section-interval 35-1 (Henry House Falls) are different, having regular corallite size distributions and densely spaced tabulae (Pl. 18, figs. 4, 5); their growth forms are tabular (see *Paleofavosites adaensis*, p. 40).

Discussion. — These coralla are assigned to a new species, *Paleofavosites adaensis.* This species is an early member of a group of large-corallite favositids similar to *Favosites gothlandicus* Lamarck. Members of this group occur from the earliest Silurian (earliest Llandovery) until the early Late Silurian (Ludlow), and possible members occur both earlier and later. Position of pores varies within this group, but other characters are quite consistent. These include thin walls, short septa, and corallites of large size and regular size distribution.

Some of the Ordovician corals described as *Paleofavosites capax* are similar to members of this group. The most similar is Bolton's (1980, pp. 22, 25, pl. 2.7, figs. 1, 5, 6) material from the Burmingham Member of the White Head Formation near Percé, Québec (Upper Ordovician, Ashgill, pre-Hirnantian; see Skidmore and Lespérance, 1981, p. 38; Lespérance *et al.*, 1987, fig. 4). It has adult corallites with dimensions of 3.3–4.0 mm, thin walls, and some mid-wall pores, and lacks septal spines, but differs from *P. adaensis* by having much more abundant small corallites on transverse sections. Other corals referred to *P. capax* are listed in the *Discussion* under *P. subelongus* (pp. 87, 88).

Among other Early Llandovery species, *P. adaensis* is most similar to *Paleofavosites* sp. of Bolton (1981b, pl. 1, fig. 3), from the Clemville Formation of the southern Gaspé Peninsula, Québec (Lower–Middle Llandovery, Rhuddanian–lower Aeronian; Nowlan, 1983, fig. 2, termed Rhuddanian–Idwian therein). Bolton's species has similar thin-walled corallites of regular size, but these are slightly smaller with dimensions of about 2.5–3.3 mm, and appear to have corner pores only.

Another similar species is *Palaeofavosites* [*sic*] *oelaensis* Klaamann (1959, p. 259, pl. 2, figs. 3, 4), from the Juuru Stage of Estonia (Rhuddanian), also described and illustrated by Stasinska (1967, p. 71, pl. 14, figs. 1a, 1b, table 4) from Spirodden, Asker district of Norway (Llandovery 6cα: lower Aeronian; upper Solvik Formation?; Worsley *et al.*, 1983, fig. 5). Klaamann's and Stasinska's coralla have corallites with dimensions of 2.6–4.2 mm and 1.5–4.2 mm, respectively, and possess both mid-wall and corner pores. They differ from *P. adaensis* by apparently having common, short septal spines, and corallites that may have variable sizes and shapes in transverse section. *Favosites ingens* Klaamann (1962, pp. 162, 163, pl. 5, figs. 1, 2) from the Adavere Stage of Estonia (Upper Llandovery, Telychian), also described and illustrated by Stasinska (1967, pp. 80, 81, pl. 20, figs. 1–4) from the Upper Llandovery of Ringerike and Malmøy, Norway (Series 7), has mid-wall pores only, and large corallites with dimensions of about 4.0–8.0 mm.

Copper (1978, pl. 10, figs. 4, 5) illustrated a coral identified as *Favosites* sp. from the Fossil Hill Formation of Manitoulin Island, Ontario (Telychian; Brett *et al.*, 1991, fig. 5). This species has large, thin-walled corallites with regular dimensions of about 5–6 mm. Pores could not be recognized in the photographs, but the assignment to *Favosites* suggests that it lacks the corner pores characteristic of *P. adaensis.*

Palaeofavosites [*sic*] *asper* var. *maxima* Chernyshev (1937, p. 84, pl. 6, fig. 5) from the Upper Silurian of Novaya Zemlaya has also been described and illustrated as *Palaeofavosites* [*sic*] *maximus* by Kokscharskaya (in Volkova *et al.*, 1978, pp. 41, 42, pl. 9, figs. 1a, 1b) from the Kuranakhinskiy Horizon of Verkhoyan, Siberia (Lower–Middle Llandovery). Chernyshev's material has corallites of regular size with diameters of about 4–5 mm, and weak septa, but other features are difficult to determine. Kokscharskaya's specimens have corallites with dimensions of 3.5–4.2 mm, and some mid-wall pores, but they are distinguished from *P. adaensis* by having non-crenulate tabulae, thicker walls, and small corallites that are more abundant.

The neotype of *Favosites gothlandicus,* from the Mulde Marl of Gotland, Sweden (upper Lower Silurian, Upper Wenlock), was described and illustrated by Jones (1936, pp. 8, 9, pl. 1, figs. 1, 2) and by Lafuste and Tourneur (1988, pp. 189–198, figs. 1–4, pl. 1, figs. 1–4, pl. 2, figs. 1–3). This corallum is somewhat similar to *P. adaensis,* having corallites of regular size with thin walls and lacking septa, but has smaller corallites with dimensions commonly 2.0–2.7 mm and sometimes up to 3.2 mm, and mid-wall pores only. Many of the other Late Llandovery, Wenlock, and Ludlow corals that have been assigned to *F. gothlandicus* by various authors bear some similarity to *P. adaensis,* but all are distinguished from it by their lack of corner pores. The true nature of all material previously described as *F. gothlandicus* presents a substantial taxonomic problem that is outside the scope of the present study.

Within the group of large-corallite favositids similar to *F. gothlandicus,* a transition in position of pores occurred through time. The earliest species, including *P. adaensis,* are members of *Paleofavosites* possessing only corner pores or a combination of corner and mid-wall pores. Later species have exclusively mid-wall pores and belong to *Favosites.* It is quite possible that the change in pore position in this lineage occurred independently from parallel changes taking place in other favositids.

Among the other species occurring in the east-central United States, *P. adaensis* is most similar to *Paleofavosites* sp. cf. *P. ivanovi.* The latter species occurs in the Bowling Green Dolomite of west-central Illinois and northeastern Missouri, and is of approximately equivalent age to *P. adaensis* (*i.e.,* late Rhuddanian). It is distinguished from *P. adaensis* by its smaller corallites (see Text-fig. 27; Table 19), less regular corallite size distributions on transverse sections, and much rarer mid-wall pores.

Paleofavosites adaensis was listed by Elias and Young (1992, fig. 2) as *Paleofavosites* n. sp. A, and by Young and Elias (1993) as *Paleofavosites* n. sp.

Occurrences.—Lower Lower Silurian (Lower Llandovery, upper Rhuddanian): upper Mosalem Formation, northwestern Illinois. Lower Lower Silurian (Lower? Llandovery, upper Rhuddanian?): Cochrane Formation, south-central Oklahoma; Sexton Creek Limestone, southern Illinois.

Holotype.—USNM 485936 (Pl. 18, figs. 1–3), site 23i, interval 23-5, Cochrane Formation, Section 23 (Lawrence Quarry), Pontotoc County, Oklahoma.

Paratype.—USNM 485937 (Pl. 18, figs. 4–8), interval 35-1, Cochrane Formation, Section 35 (Henry House Falls), Carter County, Oklahoma.

Other material described above.—Six specimens: USNM 485938, site 23i, interval 23-5, Cochrane Formation, Section 23 (Lawrence Quarry), Pontotoc County, Oklahoma; USNM 485939, 485940, interval 35-1, Cochrane Formation, Section 35 (Henry House Falls), Carter County, Oklahoma; UI C-1347, C-1351, collected by T. E. Savage (labelled "*Favosites favosus* Goldfuss, Sexton Creek [Formation], Alexander Co., Ill."), Sexton Creek Formation, Alexander County, Illinois; USNM 485941, interval 10-3, Mosalem Formation, Section 10 (Lost Mound), Jo Daviess County, Illinois.

Paleofavosites species
cf. **P. ivanovi** Sokolov, 1951a
Plate 19, figures 1–7

[*cf.*] *Palaeofavosites ivanovi* Sokolov, 1951a, pp. 37, 38, pl. 3, figs. 2, 3; Sokolov and Tesakov, 1963, p. 43, pl. 2, figs. 1, 2.
[?] *Paleofavosites capax* (Billings, 1866). Bolton, 1981a, pl. 9, fig. 10.

Description.—Growth form can be examined in one corallum (USNM 485942). It has a low domical form, and is more than 27 mm wide and 19 mm high.

In transverse section, corallites are usually regular polygons (Pl. 19, fig. 1). Average corallite dimensions are variable on each transverse section (Text-fig. 30A): overall range is 0.50–4.25 mm; average dimensions of adult corallites are commonly 2.7–4.0 mm (Table 19). Mean corallite areas on transverse sections are about 5–6 mm^2 (Table 19). Corallites may have three to ten sides (Table 19); shapes are variable on each transverse section, reflecting the variability of average dimensions (Pl. 19, figs. 1, 7; see Text-fig. 30A, B). Corallites at the colony margin have flat outlines where they are in contact with other individuals, but are curved on their free sides (Pl. 19, fig. 2). In longitudinal section, corallites curve gently away from the colony axis (Pl. 19, fig. 6).

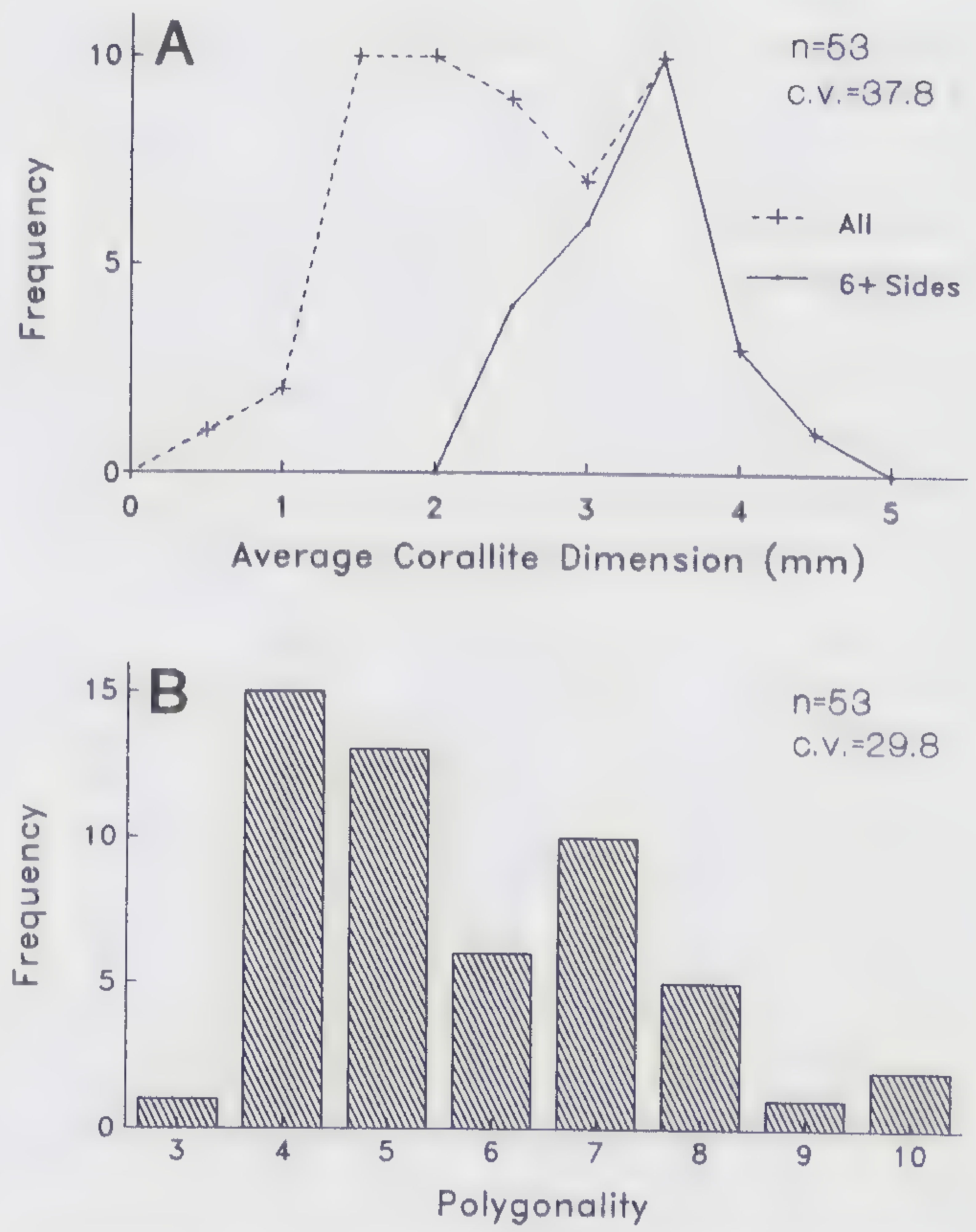
Corallite walls are straight or curved in transverse section, rarely wavy (Pl. 19, fig. 4). Walls are thin, 0.05–0.10 mm thick (Table 19); thickness is regular. In longitudinal section, walls are straight or wavy (Pl. 19, figs. 3, 6). Corner pores are moderately common; they are simple, with diameters of 0.075–0.175 mm (Table 19). The end of a wall adjacent to a pore may be square. Corner pores usually have thin pore plates that are straight or are broadly curved into corallite lumina. Mid-wall pores located a short distance in from the wall corner occur in a few corallites.

Septa are generally absent, but short, slender septal spines are developed locally in zones that show slight cyclomorphic thickening. In longitudinal section, spines are straight, and are directed slightly upward adaxially (Pl. 19, fig. 6). Average length of septa is 4% of corallite radius (Table 19). Tabulae are moderately thin, flat or wavy, and may have lobe-like axial depressions (Pl. 19, figs. 3, 6). They are usually complete. Some tabulae are crenulate, appearing as curved plates along the corallite wall in transverse section (Pl. 19, fig. 4). Tabulae are very widely spaced, about two in 5 mm (Table 19).

Discussion.—These coralla are comparable to *Palaeofavosites* [*sic*] *ivanovi* from the Upper Ordovician of the west slopes of the Urals (Sokolov, 1951a), and from the Upper Ordovician (mid–upper Ashgill) Burskiy Horizon (Bur Formation; Kanygin *et al.*, 1988, p. 11) of the Siberian Platform (Sokolov and Tesakov, 1963). As described and illustrated, *P. ivanovi* has corallites of variable size, the larger ones with dimensions of about 2.5–3.5 mm, and appears to have only rare, short septa. It differs from our coralla by having thicker walls, tabulae that are generally more densely spaced, and larger corner pores. Specimens from the east-central United States are therefore identified as *Paleofavosites* sp. cf. *P. ivanovi.*

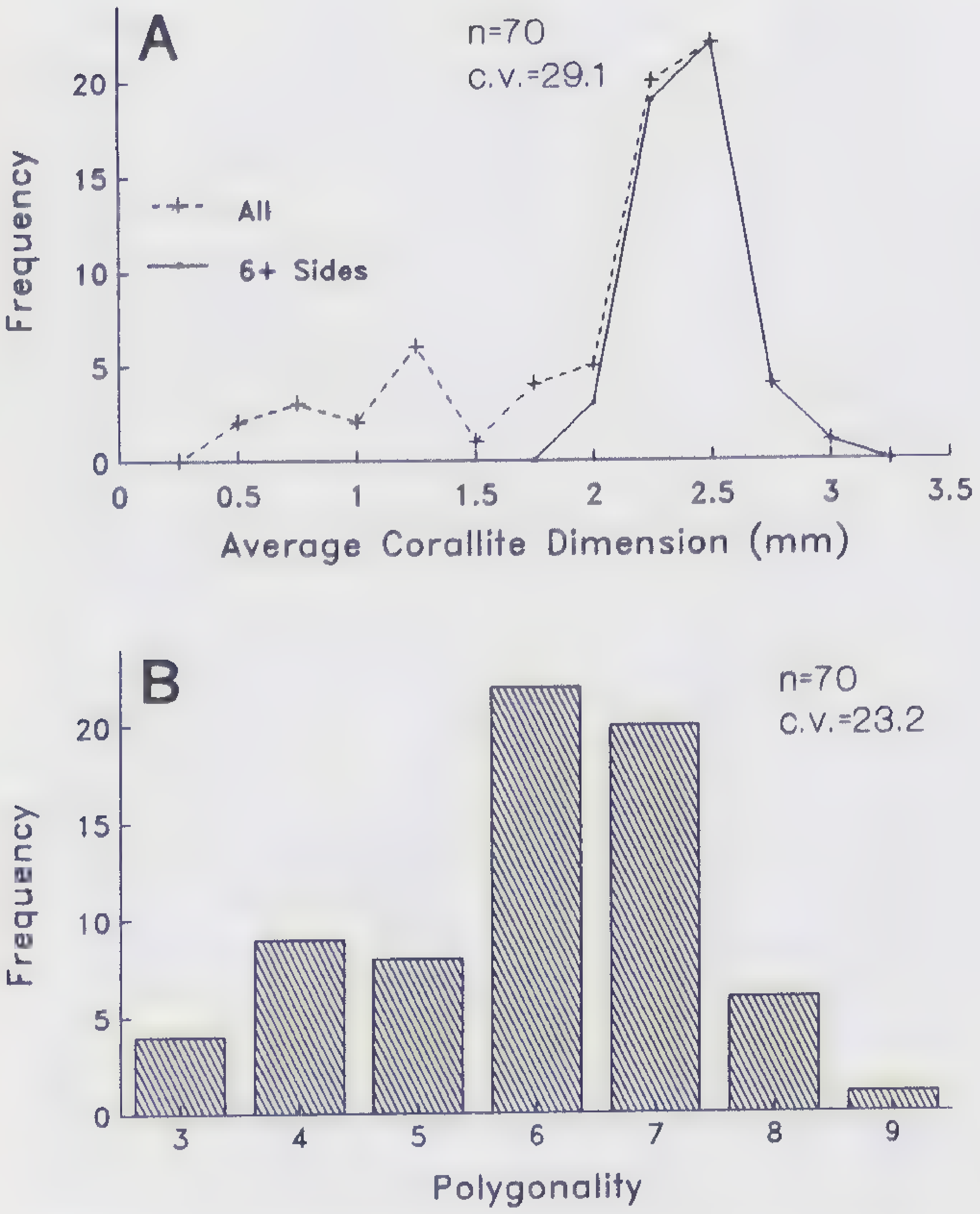
Our material is very similar to, and is questionably synonymized with a corallum from the Gun River Formation of Anticosti Island, Québec (lower Lower Silurian, Middle Llandovery, lower Aeronian; Barnes, 1988, fig. 2), illustrated as *Paleofavosites capax* by Bolton (1981a). We examined that specimen, collected by Bolton in 1975 (GSC 66875); like *Paleofavosites* sp. cf. *P. ivanovi,* it also has corallites of variable size, short and rare septa, thin walls, and broadly spaced crenulate tabulae, but differs by having more abundant mid-wall pores and smaller corallites (biometric data: ACD (all) = 1.92 mm, ACD (6+) = 2.63 mm, CoA = 3.85 mm^2, Pol = 6.1, WT = 0.106 mm, LS = 0%, Ta5 = 1.4; compare with Table 19; see Text-fig. 27).

Other similar species include *Palaeofavosites* [*sic*] *alveolaris* (Goldfuss) and *Palaeofavosites* [*sic*] *spirodensis* Stasinska, as documented by Stasinska (1967, pp. 67, 72, table 4, pl. 15, figs. 2, 3a, 3b, 4a–c) from the Llandovery Series 6 of Norway (Lower–Middle Llandovery, Rhuddanian–lower Aeronian; Worsley *et al.*, 1983, fig. 5, termed Rhuddanian–Idwian therein). These species have corallites of variable size, crenulate tabulae, and short, thin septa; they may be conspecific with one another. They differ from *Paleofavosites* sp. cf. *P. ivanovi* by having smaller corallites with dimensions of about 2.5–3.0 mm, and more densely spaced tabulae. *Palaeofavosites* [*sic*] *alveolaris* (Lonsdale), as described and illustrated by Nelson (1963, pp. 51, 52, pl. 7, fig. 9) from member 3 and the upper member of the Caution Creek Formation and from members 1 and 2 of the Chasm Creek Formation of northern Manitoba (Upper Ordovician, Richmondian; see Elias, 1991, fig. 3), is quite different, having corallites of regular size and shape (see *Discussion* under *Paleofavosites* sp. A, p. 96).



Text-figure 30.—Frequency distributions of average corallite dimension (all corallites and those with six and more sides) and polygonality for one corallum of *Paleofavosites* sp. cf. *P. ivanovi.* **A, B,** USNM 485943, Section-interval 17-1a (Clarksville). Both graphs represent the same transverse section; n = number of corallites (all), c.v. = coefficient of variation for all corallites.

Among the other species occurring in the uppermost Ordovician and lowermost Silurian of the east-central United States, *Paleofavosites* sp. cf. *P. ivanovi* has some similarities to both the older *Paleofavosites subelongus* and to *Paleofavosites adaensis,* which is of approximately equivalent age. *Paleofavosites subelongus* also tends to have corallites of variable size, but these are somewhat smaller than those of *Paleofavosites* sp. cf. *P. ivanovi* (Text-fig. 27) and have thicker walls and longer, more abundant septa. *Paleofavosites adaensis* is similar to *Paleofavosites* sp. cf. *P. ivanovi* in having thin walls and septa that are weak or absent, but has larger corallites (Text-fig. 27) that are usually of regular size, and more abundant mid-wall pores.



Text-figure 31.—Frequency distributions of average corallite dimension (all corallites and those with six and more sides) and polygonality for one corallum of *Paleofavosites* sp. A. **A, B**, USNM 485947, Section-interval 6-1 (Plaines West). Both graphs represent the same transverse section; n = number of corallites (all), c.v. = coefficient of variation for all corallites.

Occurrences.—Lower Lower Silurian (Lower Llandovery, upper Rhuddanian): Bowling Green Dolomite, northeastern Missouri and west-central Illinois.

Possibly in lower Lower Silurian (Middle Llandovery, lower Aeronian): Gun River Formation, Anticosti Island, Québec.

Material described above.—Two specimens: USNM 485942, interval 36-1, Bowling Green Dolomite, Section 36 (Indian Creek), Calhoun County, Illinois; USNM 485943, interval 17-1a, limestone facies at base of Bowling Green Dolomite, Section 17 (Clarksville), Pike County, Missouri.

Paleofavosites species A
Plate 19, figures 8–12

Description.—Coralla have tabular and low domical growth forms (Table 14). Size range is 47–115 mm wide and 14–40 mm high.

In transverse sections, corallites appear as polygons of regular or slightly irregular shape (Pl. 19, figs. 9, 11). The overall range of average corallite dimensions is 0.55–2.82 mm; adult corallites commonly have average corallite dimensions of 2.0–2.7 mm (Table 19). Mean corallite areas on transverse sections are about 3–4 mm^2 (Table 19). On transverse sections, most corallites have regular sizes and have five to seven sides; corallites may rarely have up to nine sides (Pl. 19, figs. 9, 11; Text-fig. 31A, B; Table 19). Offsets are relatively rare, and commonly have three or four sides; sides were added during growth. There is little variation among the studied coralla in average corallite dimensions (Text-fig. 27). In longitudinal section, corallites are straight or slightly curved.

Corallite walls are straight or gently curved in transverse section (Pl. 19, fig. 9). Walls are thin; 0.050–0.125 mm thick (Table 19). Walls are straight or wavy in longitudinal section (Pl. 19, figs. 10, 12). Corner pores are simple, and mid-wall pores may occur, but poor preservation prevents detailed observation. Septa are generally absent (Table 19); short, thick septal spines occur rarely. Tabulae are strongly crenulate; concave in corallite corners, and at midpoint of wall in large corallites (Pl. 19, fig. 8). Spacing of tabulae is variable, averaging about four in 5 mm (Table 19). In some coralla, spacing of tabulae shows well-developed cyclomorphic variation; in one corallum, pairs of closely spaced and widely spaced bands average 18.5 mm in thickness (Table 19; Pl. 19, fig. 12).

Discussion.—These coralla are identified as *Paleofavosites* sp. A; their poor preservation prevents a definite specific assignment and makes comparisons with other species difficult. They are probably most similar to *Palaeofavosites* [*sic*] *argutus* Ivanov (1950, p. 14, pl. 3, figs. 1, 2) from the Upper Ordovician of the Urals, also described and illustrated by Sokolov and Tesakov (1963, pp. 40, 41, pl. 1, figs. 1, 2) from the Upper Ordovician of the Siberian Platform. Both of those studies described corals with corallite dimensions of about 2.0–2.5 mm. It is difficult to determine details from Ivanov's illustrations; Sokolov and Tesakov's material has corallites of regular size with a very similar appearance to those of *Paleofavosites* sp. A, but may have thicker walls.

Paleofavosites sp. A is also similar to *Palaeofavosites* [*sic*] *alveolaris* as described and illustrated by Nelson (1963, pp. 51, 52, pl. 7, fig. 9) from member 3 and the upper member of the Caution Creek Formation and from members 1 and 2 of the Chasm Creek Formation of northern Manitoba (Upper Ordovician, Richmondian; see Elias, 1991, fig. 3). Nelson's material has corallites of regular size and apparently lacks septa, but the corallites are slightly larger (dimensions of about 2.5–3.0 mm) than those in our specimens, and the tabulae are described as flat, not crenulate. *Paleofavosites* sp. A is not similar to the *Palaeofavosites* [*sic*] *alveolaris* described and illustrated by Stasinska (1967,

p. 67, pl. 15, figs. 2, 3a, 3b, table 4) from the Llandovery Series 6 of Norway (lower Lower Silurian, Lower–Middle Llandovery, Rhuddanian–lower Aeronian; Worsley *et al.,* 1983, fig. 5, termed Rhuddanian–Idwian therein) (see *Discussion* under *Paleofavosites* sp. cf. *P. ivanovi,* p. 95).

Paleofavosites sp. A is somewhat similar to, and may have been descended from, the older *Paleofavosites subelongus,* which occurs in the uppermost Ordovician and lowermost Silurian of the east-central United States. It is distinguished from *P. subelongus* by its regular-sized, large corallites, generally thinner walls and rare or absent septa, and typically lower growth forms.

Occurrence.—Lower Lower Silurian (Lower–Middle Llandovery, upper Rhuddanian–lowermost Aeronian): Elwood Formation, northeastern Illinois.

Material described above.—Eight specimens: USNM 485944, 485945, interval 5-2, Elwood Formation, Section 5 (Schweizer North), Will County, Illinois; USNM 485946–485951, interval 6-1, Elwood Formation, Section 6 (Plaines West), Will County, Illinois.

Order **AULOPORIDA** Sokolov, 1947

Superfamily **AULOPORICAE**
Milne-Edwards and Haime, 1851

Family **AULOPORIDAE**
Milne-Edwards and Haime, 1851

Genus **AULOPORA** Goldfuss, 1829

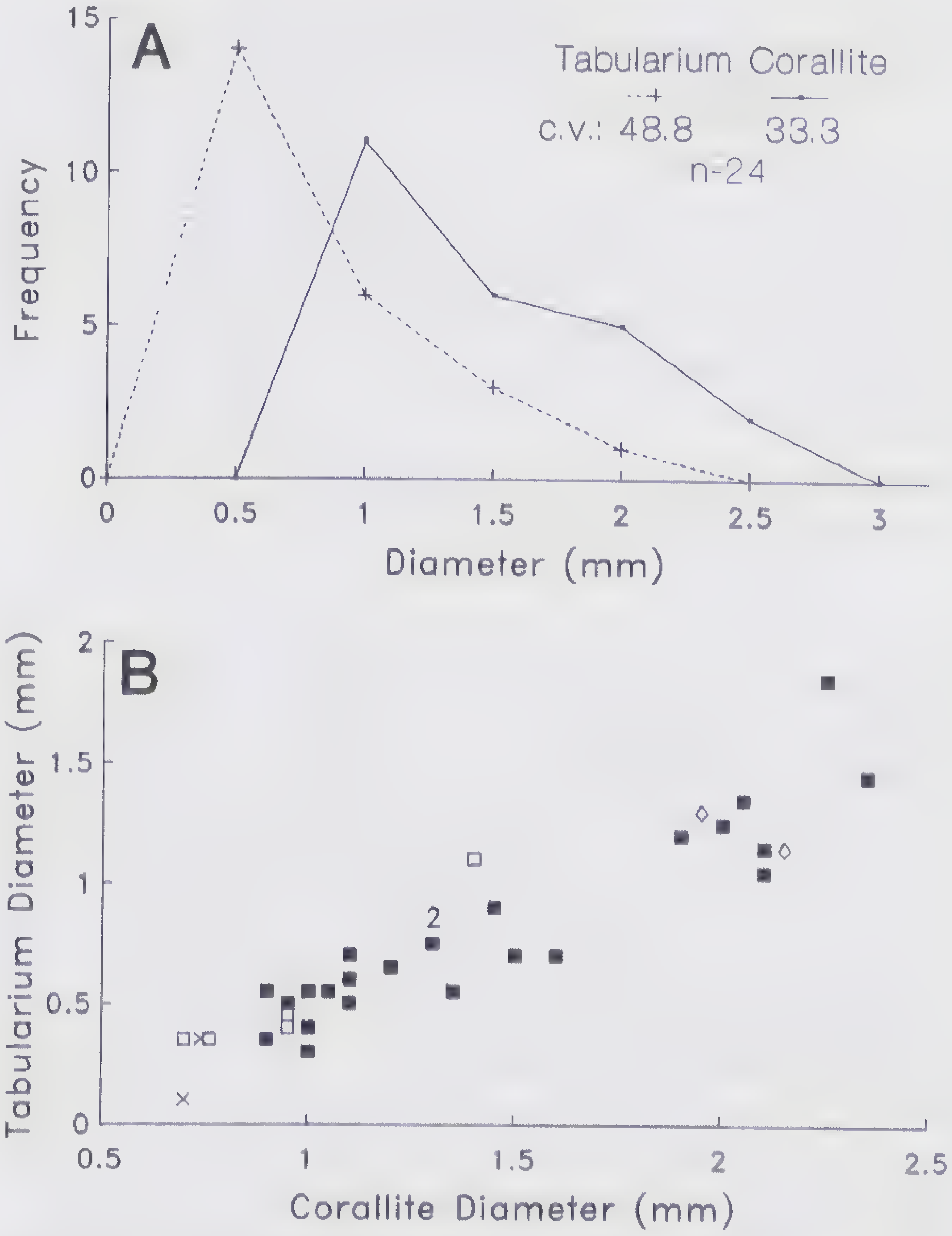
Aulopora Goldfuss, 1829, p. 82.

Type species.—By subsequent designation (Milne-Edwards and Haime, 1850, p. lxxvi): *Aulopora serpens* Goldfuss (1829, p. 82, pl. 29, fig. 1b); Middle Devonian, Bensberg of the Eifel District, Germany.

Diagnosis.—"Corallum reptant, low, commonly adherent; corallites cornute, joined in linear chains or anastomosing; calices slightly raised above substrate, conical or barrel-shaped; walls moderately thick; septal spinules present or absent; tabulae commonly absent, or sparse and oblique; increase basal-lateral; offsets originate on calical surface of wall" (Hill, 1981, p. F631).

Aulopora species A
Plate 20, figures 1–10

Description.—Coralla are reptant in form, umbelliferous in places, and small (Text-fig. 32B). Both of the specimens from Section 23 (Lawrence Quarry) appear to include several small coralla comprising only one or a few corallites. In thin section, corallites are rarely observed to be connected with one another (see Pl. 20, figs. 1, 7, 10); most appear to be immature. In some cases, it is not possible to determine spatial relationships due to extreme variation in orientation of the encrusted substrates. Coralla often encrust other skeletons, including those of *Halysites alexandricus* and calcareous algae (Pl. 20, fig. 1).



Text-figure 32.—Intraspecific variation in *Aulopora* sp. A. **A**, Tabularium and corallite size-frequency distributions; specimen USNM 485785d, Section-interval 23-2 (Lawrence Quarry). n = number of corallites, c.v. = coefficient of variation. **B**, Relationship between tabularium diameter and corallite diameter in specimens from the east-central United States and comparative material of *Aulopora* from Anticosti Island, Québec. Each data point represents a single corallite except as otherwise stated. Symbols for specimens: □ USNM 485780d, Section-interval 23-2 (Lawrence Quarry); n (number of corallites) = 5; ■ USNM 485785d, Section-interval 23-2 (Lawrence Quarry); n = 24 (two corallites plot at the point labelled "2"); ◇ USNM 485952, Section-interval 37-1 (Essex); n = 2; × GSC 111438, Ellis Bay Formation, Anticosti Island, Québec; n = 2.

In transverse section, corallites are subcircular or subovate in shape (Pl. 20, figs. 5, 8, 9). Tabularium and corallite diameters are both variable; the former are 0.30–1.85 mm, the latter 0.70–2.35 mm (Table 20). In longitudinal section, corallites are commonly short; five measured individuals are about 1.6–8.0 mm long. They may be moderately or highly curved, occasionally geniculate (Pl. 20, figs. 2, 10). Basal parts and lower sides of corallites conform to the shapes of their substrates (Pl. 20, figs. 1–4). Corallites generally expanded

Table 20.—Biometric data for *Aulopora* sp. A from the east-central United States. *TaD* = tabularium diameter, *CoD* = corallite diameter, *WT* = wall thickness, *LS* = length of septa; s.d. = standard deviation, c.v. = coefficient of variation.

	parameters			
data	*TaD*	*CoD*	*WT*	*LS*
mean	0.85 mm	1.48 mm	0.312 mm	11%
range of specimen means	0.53–1.22 mm	0.95–2.05 mm	0.185–0.412 mm	0–22%
s.d. of specimen means	0.35 mm	0.55 mm	0.116 mm	16%
c.v. of specimen means	41.2	37.2	37.2	141.4
minimum	0.30 mm	0.70 mm	0.150 mm	—
maximum	1.85 mm	2.35 mm	0.725 mm	—
mean intraspecimen c.v.	54.6	31.4	27.2	—
no. of specimens studied	3	3	3	2

rapidly following initiation; this occurred both in separated, single corallites and in corallites that were produced by offsetting (Pl. 20, figs. 1, 2).

Corallite walls are of variable thickness, thick to very thick, about 0.2–0.4 mm (Table 20). Each wall is composed of two layers. The outer layer is darker, thin or very thin, and appears to have a lamellar structure. The inner layer is paler and thicker, and is concentrically lamellar in transverse section (Pl. 20, fig. 6). In longitudinal section, lamellae of the inner layer may have a wavy appearance (Pl. 20, fig. 3).

Septa are spinose, thorn-like with thickened bases, and slightly upward-directed in longitudinal section (Pl. 20, figs. 3, 6). They are usually sparsely distributed, but may be absent or common in individual corallites (Pl. 20, figs. 2, 5, 7). Septa are usually short, with lengths averaging 11% of tabularium radius (Table 20). Septa are the same color as the lamellar inner wall, and their structure appears to extend from that of the wall. Tabulae are very rare, thin, subhorizontal or slightly convex.

Intraspecific variation.—Although only three specimens are known, there is considerable intraspecific variability in size and in development of skeletal elements (Table 20). A frequency distribution of tabularium and corallite diameters for what appear to be several small coralla in one specimen from Section 23 (Lawrence Quarry) shows a majority of small corallites, with a gradual decrease in numbers with increased size (Text-fig. 32A). This is consistent with the interpretation that most corallites are immature (see also *Aulopora* sp. A, p. 40).

A graph of tabularium diameter *versus* corallite diameter shows that the relationship between these characters is consistent between all specimens (Text-fig. 32B). The specimen from Section 37 (Essex) has corallites that are in the same size range as the larger corallites from Section 23 (Lawrence Quarry). The discontinuity in the data between large and small corallites (Text-fig. 32B) is probably an artifact of the small sample size. There are no obvious differences between specimens or localities in other characters, including corallite shape, wall thickness, and form of septa and tabulae.

Discussion.—As a group, Ordovician and Silurian members of *Aulopora* are poorly understood. In most cases, species have been described only where external surfaces are preserved in three dimensions, with an emphasis on characters such as branching pattern and form of epitheca; internal structures of most are not known (Scrutton, 1990, p. 61). Since auloporids are morphologically extremely simple, this leaves very few points of reference that would permit comparison of those species with thin-sectioned material such as described here. As noted by Webby (1977, p. 175), there has been confusion between *Aulopora* and "gregarious commensal" forms of the family Cornulitidae Fisher, which includes problematic conoidal shells. This confusion was caused by the examination of external surfaces only, since the vesicular wall structure of cornulitids (Fisher, 1962, p. W137, fig. 78) is quite different from the lamellar structure of auloporids. Two of the specimens described above are from the Keel Formation of south-central Oklahoma, a unit in which problematic conoidal shells of the family Tentaculitidae Walcott are also known to occur. The latter are easily distinguished in thin section by their longitudinally striate walls with parallel fibrous structure.

The coralla described above are identified as *Aulopora* sp. A; they are not assigned to a new species because only a few specimens are known and aspects of colony growth are poorly understood. Among other species of comparable age, *Aulopora* sp. A is probably most similar to *Aulopora ellisensis* Twenhofel (1928, p. 124, pl. 2, fig. 14), from the upper part of member 3 of the Ellis Bay Formation on Anticosti Island, Québec (zone 4 of Twenhofel: uppermost Ordovician, Gamachian; Petryk, 1981, fig. 4). We examined the holotype of *A. ellisensis,* which was collected by Twenhofel (YPM 20501). It consists of two corallites exposed in three-dimensions; these are geniculate, rapidly expanding, about 6 to more than 7 mm long, with diameters of about 1 mm, thin walls at the calice rims, and smooth epithecae. Two other auloporid corallites in a specimen from Anticosti that we examined are also similar to *Aulopora* sp. A (GSC 111438; collected by A. A. Petryk in 1983, from a bioherm in member 7 of the Ellis Bay Formation at Point Laframboise). These corallites are smaller than those of *Aulopora* sp. A. They have lamellar walls, thick spinose septa, and the following measured characters: TaD = 0.10–0.35 mm, CoD = 0.70–0.75 mm, WT = 0.20–0.25 mm, LS = 0–50% (compare with Table 20; see Text-fig. 32B).

Two older species have characters similar to those of *Aulopora* sp. A. One is *Aulopora* (?) *trentonensis* Winchell and Schuchert (1895, p. 95, pl. G, figs. 26–28), from the "Trenton Shales" of Minnesota (Decorah Shale according to Bassler, 1950, p. 15), which are of Middle Ordovician, Rocklandian to Shermanian age (Sloan, 1987, fig. 2.6). It has rapidly expanding corallites about 2 mm long and 1 mm in diameter, but these apparently lack septal spines and tabulae. The other species is *Aulopora walliensis* Webby (1977, p. 175, pl. 8, figs. 1–7), from the upper Cliefden Caves Limestone of central-western New South Wales, Australia (Ordovician, Caradoc; Webby *et al.*, 1981, pl. 1). It has corallites with diameters of 1.6–2.2 mm and walls that are 0.2–0.4 mm thick. However, it is distinguished from *Aulopora* sp. A by its parallel, close-spaced, almost fasciculate corallites, and by its apparently specialized mode of life as a commensal on brachiopod shells.

Among younger species that share some characters with *Aulopora* sp. A is *Aulopora* sp. of Bolton (1981a, pl. 10, fig. 7), from the Jupiter Formation of Anticosti Island (lower Lower Silurian, Middle–Upper Llandovery, upper Aeronian–Telychian; Barnes, 1988, fig. 2). *Aulopora* sp. has corallite diameters of about 1.0–1.5 mm and has a reptant growth form, but few other features can be determined. *Aulopora assueta* Klaamann (1966, pp. 66, 67, 93, pl. 21, figs. 4, 5), from the Adavere Stage of Estonia (Upper Llandovery), has thick-walled corallites with diameters up to 2 mm and lengths of 4.5–5.0 mm, that may be reptant or upright. *Aulopora assueta* has weak septa, but it differs from *Aulopora* sp. A in lacking tabulae. *Aulopora enodis* Klaamann (1966, pp. 67, 68, 94, pl. 19, figs. 8, 9, pl. 21, fig. 1), from the Jaagarahu Stage of Estonia (upper Lower Silurian, mid-Wenlock), has a reptant form, corallites that are 4–6 mm long, and short septa, but its corallite diameters of 0.7–1.0 mm are somewhat smaller than is typical of *Aulopora* sp. A.

Occurrences.—Uppermost Ordovician (Gamachian): lower Keel Formation, south-central Oklahoma. Uppermost Ordovician (?; Gamachian?) to lowermost Silurian (Lower Llandovery, lower Rhuddanian): Wilhelmi Formation, northeastern Illinois.

Material described above.—Three specimens: USNM 485780d, 485785d, site 23iv, interval 23-2 (*Brevilamnulella* beds), Keel Formation, Section 23 (Lawrence Quarry), Pontotoc County, Oklahoma; USNM 485952, interval 37-1, Wilhelmi Formation, Section 37 (Essex), Kankakee County, Illinois.

Order **TETRADIIDA** Okulitch, 1936

Family **TETRADIIDAE** Nicholson, 1879

Genus **RHABDOTETRADIUM** Sokolov, 1955

Rhabdotetradium Sokolov, 1955, p. 247.

Type species.—By original designation: *Rhabdotetradium nobile* Sokolov (1955, p. 248, pl. 57, figs. 1–4); Dolborskaya Horizon (Dolbor Formation: Upper Ordovician, lower Ashgill; Kanygin *et al.*, 1988, pp. 11, 12), Siberian Platform.

Diagnosis.—Tetradiidae with phaceloid coralla. Corallites prismatic to subcircular in outline. Increase quadripartite, corallites diverged after increase. Tabulae rare or absent. (After Hill, 1981, p. F522.)

Remarks.—*Rhabdotetradium* was erected by Sokolov (1955) to include phaceloid tetradiid species; such corals had previously been placed by Bassler (1950, pp. 279–283) in his "*Tetradium syringoporoides* Group." Sokolov's distinction of tetradiid genera has since been disputed by Webby and Semeniuk (1971, pp. 249–251), who argued that growth style was not a valid discriminator, and that *Rhabdotetradium* and the other genera of Sokolov should be considered junior synonyms of *Tetradium* Dana. As Hill (1981, p. F521) pointed out, however, ecophenotypic aspects of tetradiid growth have not been sufficiently investigated. At present, we prefer to maintain the separation of these genera.

Rhabdotetradium species A

Plate 20, figures 11–17

Description of coralla.—All material is fragmentary, so it is not possible to determine larger scale aspects of colony form. Coralla have branching growth forms; each branch is composed of a single corallite except in portions representing corallite increase.

In transverse section, corallites are subcircular to subquadrate or diamond-shaped in outline (Pl. 20, figs. 11–14). They are small, with corallite diameters of 0.40–0.80 mm and tabularium diameters of 0.25–0.65 mm. Walls are moderately thin, 0.05–0.10 mm thick. Walls have a radially fibrous microstructure. Corallites not undergoing increase have four triangulate, apparently laminar septa with slender tips (Pl. 20, figs. 12–14). Lengths of septa are generally about 25% of the corallite radius. Longitudinal sections of corallites cannot be prepared from the available material.

Corallite increase.—Increase was axial, quadripartite, and complete. Prior to division, septa of the parent corallite increased in length to form complete partitions that meet at the axis (Pl. 20, fig. 15). The chambers formed by partitioning developed into four small, subcircular, contiguous, apparently aseptate corallites with corallite diameters of about 0.40–0.45 mm (Pl. 20, fig. 16).

With continued vertical growth, these contiguous corallites developed into separate, broadly divergent, subcircular corallites (Pl. 20, fig. 17). Adjacent individuals with corallite diameters of 0.30–0.40 mm are 0.075 mm apart, and opposite individuals are 0.175 mm apart. At this diameter, corallites possess short, stubby septa with lengths of about 0.05 mm; these septa are oriented so that they point toward the adjacent corallites.

Discussion.—These coralla are identified as *Rhabdotetradium* sp. A; a specific name is not assigned because of the small number and fragmentary nature of specimens. The occurrence of this species in the uppermost Ordovician (Gamachian) of North America is important because it is among the youngest known tetradiids worldwide, and it bears a strong resemblance to some other species of similar age. From the nature and location of the specimens of *Rhabdotetradium* sp. A, it is very unlikely that they were weathered out of older Ordovician rocks and redeposited in the Leemon Formation. Matrix within the calices and between corallites is identical in appearance to common Leemon lithologies, and the corallites are not severely abraded. Tetradiids are not known from the underlying Girardeau Limestone (uppermost Ordovician, Gamachian) and Orchard Creek Shale (Upper Ordovician, Richmondian). From the Blackriveran (Middle Ordovician) Plattin Limestone of Cape Girardeau, Missouri, Bassler (1950, pp. 14, 281) listed *Tetradium syringoporoides* Ulrich (= *Rhabdotetradium syringoporoides*), but that species typically has somewhat larger corallites than does *Rhabdotetradium* sp. A.

The history of tetradiids has been discussed by Webby and Semeniuk (1971, p. 251). Of the species described up to that date, they considered *Rhabdotetradium frutex* Klaamann (1966, pp. 19, 89, fig. 8, pl. 20, figs. 6–8), from the Porkuni Stage of Estonia (uppermost Ordovician, uppermost Ashgill), to be the youngest for which a definite age could be determined. *Rhabdotetradium* sp. A is of about the same age as *R. frutex;* both species have subcircular corallites, but those of the latter are significantly larger (corallite diameters 0.70–1.25 mm). Corallites of *R. frutex* may be separate, like those known from *Rhabdotetradium* sp. A, but they may also be arranged in rows or groups.

Rhabdotetradium sp. A is probably most similar to *Rhabdotetradium nobile* Sokolov (1955, p. 248, pl. 57, figs. 1–4) from the Dolborskaya Horizon of the Siberian Platform (Dolbor Formation: Upper Ordovician, lower Ashgill; Kanygin *et al.*, 1988, pp. 11, 12), also described by Sokolov and Tesakov (1963, p. 97, pl. 21, figs. 6, 7). Like *Rhabdotetradium* sp. A, *R. nobile* has small subcircular to subquadrate corallites with diameters of about 0.5–0.7 mm. In the latter species, however, these are often in contact in groups or short chains.

More recently, *Rhabdotetradium jiangxiense* Lin and Chow, and a subspecies, *R. jiangxiense crassum* Lin and Chow (1977, pp. 158, 159, fig. 12, pl. 39, figs. 1a–1e), have been proposed for material from the Ashgill (undivided) of Chekiang and Kiangsi provinces, China. Both of these have densely spaced subcircular corallites with appearance similar to those of *Rhabdotetradium* sp. A, but they are somewhat larger, with corallite diameters of 0.85–1.50 mm and 0.8–1.3 mm, respectively.

Several older species have corallite diameters similar to those of *Rhabdotetradium* sp. A, but their corallites tend to remain in contact following increase and commonly occur in groups or chains. Such species include: *Tetradium micropora* Bassler (1950, p. 281, pl. 1, figs. 3, 4, pl. 5, figs. 11, 12), from the Lowville Limestone of Tennessee (Blackriveran); *Tetradium oklahomense* Bassler (1950, p. 281, pl. 1, figs. 5, 5′, pl. 5, figs. 13, 13′), from the Bromide Formation of Oklahoma and the Lowville Limestone of Pennsylvania (both Blackriveran); and *Tetradium cribriforme* (Etheridge) as described and illustrated by Webby and Semeniuk (1971, pp. 253–255, pl. 17, figs. 7–12, pl. 18, figs. 1–9) from the lower Cliefden Caves Limestone, Regan's Creek Limestone, mid Bowan Park Limestone (Quondong Limestone of Webby *et al.*, 1981, pl. 1), lower Cargo Creek Limestone, and lower Reedy Creek Limestone of New South Wales, Australia (all Ordovician, Caradoc; Webby *et al.*, 1981, pl. 1).

Occurrence.—Uppermost Ordovician (Gamachian): Leemon Formation, southern Illinois and southeastern Missouri.

Material described above.—Three specimens: USNM 485770b, 485953, interval 31-1, Leemon Formation, Section 31 (Thebes North), Alexander County, Illinois; USNM 423401 (*Rhabdotetradium* sp. A is in matrix enclosing *Streptelasma leemonense*), collected by R. J. Elias and R. J. McAuley in 1983, interval 20-3, Leemon Formation, Section 20 (Short Farm), Cape Girardeau County, Missouri.

Subclass **RUGOSA**
Milne-Edwards and Haime, 1850

Order **STAURIIDA** Verrill, 1865

Suborder **STAURIINA** Verrill, 1865

Family **STAURIIDAE**
Milne-Edwards and Haime, 1850

Genus **PALAEOPHYLLUM** Billings, 1858

Palaeophyllum Billings, 1858, p. 168.

Type species.—By monotypy: *Palaeophyllum rugosum* Billings (1858, p. 168); Ordovician (Blackriveran or Trentonian), Little Discharge, Lac St.-Jean, Québec.

Diagnosis.—"Corallum phacelocerioid or phaceloid, commonly with marginal (lateral) increase; corallites with narrow peripheral stereozone formed by thickening of peripheral ends of septa; short minor septa alternate with long and somewhat wavy major septa that thin rapidly just inside stereozone, then attenuate more slowly as they approach axis, which they reach or almost reach, their axial edges being without paliform lobes; tabulae complete, commonly with axial depression and slightly downturned edges; dissepiments absent; cardinal fossula not distinct" (Hill, 1981, pp. F138, F140).

Palaeophyllum species
Plate 21, figures 1–14

Description.—Growth habits of coralla are fasciculate to cateniform (*i.e.,* with single ranks forming lacunae) or possibly tollinaform (*i.e.,* with multiple ranks and clusters at rank junctions) (Pl. 21, figs. 1–3). Larger scale aspects of colony form cannot be determined because of the fragmentary nature of material.

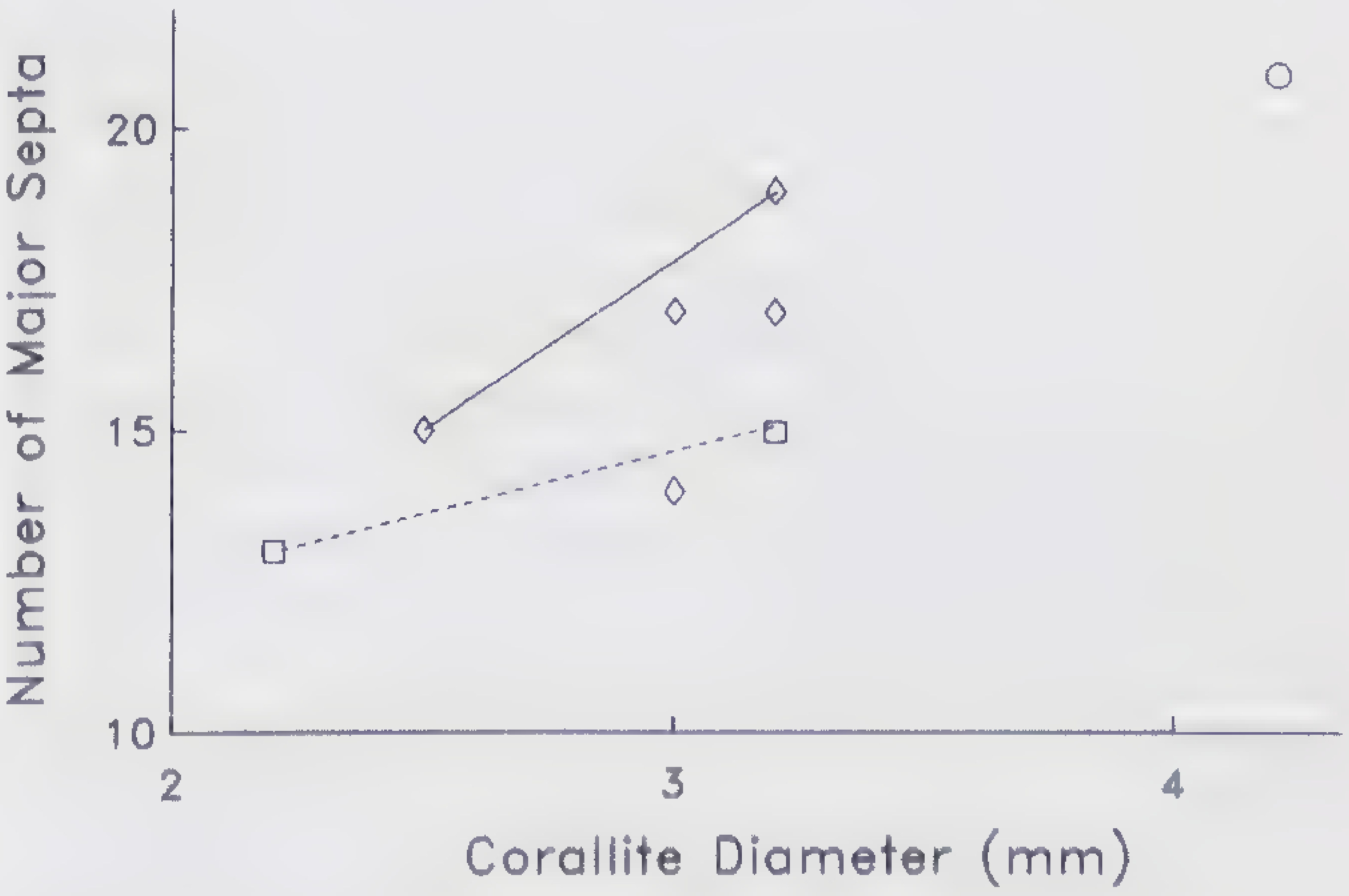
Corallites are cylindrical or subcylindrical, compressed where they come into contact with other individuals (Pl. 21, figs. 1–3, 5). Corallite diameters are 2.2–4.2 mm; most are in the range of 3.0–3.2 mm (Table 21). In longitudinal section, corallites are straight or slightly curved; known lengths are up to 10 mm, but most were probably much longer. Mode of increase is unknown.

Corallite epitheca is very thin; several corallites lack epitheca due to abrasion or corrosion. The outer surface of the epitheca is smooth; septal grooves and interseptal ridges are not seen. The stereozone is narrow to moderately wide. Thickness of the corallite wall is 0.25–0.65 mm, or about 20–30% of the corallite radius (Table 21; Pl. 21, figs. 4, 6, 8, 13). Major septa are long, 80–100% of the corallite radius; 13–21 in number, typically 15–17 (Table 21). Number of major septa is correlated with corallite size (Text-fig. 33). In transverse section, major septa are straight or curved, and may have hooked tips; they usually join together in pairs or in small groups at or near the axis (Pl. 21, figs. 5–8, 10, 11, 13). Thickness of major septa is variable, both within and between corallites; septa may taper axially or have dilated axial ends (Pl. 21, figs. 6, 7). Thickening of all major septa in a corallite tends to be associated with an increased thickness of the stereozone (Pl. 21, fig. 4). Minor septa are thinner and tapered; they are confined to the stereozone or extend beyond it to as much as 20% of the corallite radius (Pl. 21, figs. 5–8, 10, 13).

Table 21.—Biometric data for *Palaeophyllum* sp. from the east-central United States. *CoD* = corallite diameter, *WT* = wall thickness, *NS* = number of major septa, *LS* = length of major septa, *Ta5* = number of tabulae in 5 mm; s.d. = standard deviation, c.v. = coefficient of variation.

	parameters				
data	*CoD*	*WT*	*NS*	*LS*	*Ta5*
mean	3.14 mm	0.34 mm	16.4	89%	4.5
s.d.	0.60 mm	0.12 mm	2.7	6%	—
c.v.	19.1	35.3	16.5	67.4	—
minimum	2.20 mm	0.25 mm	13	80%	4
maximum	4.20 mm	0.65 mm	21	100%	5
no. of corallites studied	7	6	7	7	1

Tabulae are of moderate thickness, highly arched axially, and in some cases are concave upward peripherally (Pl. 21, figs. 9, 12, 14). Tabulae are mostly complete, rarely incomplete. They are moderately widely spaced; spacing at the corallite periphery is about 0.5–



Text-figure 33.—Relationship between number of major septa and corallite diameter in *Palaeophyllum* sp. Each data point represents a transverse thin section of a single corallite; solid line connects sections from different parts of the same corallite; dashed line connects data points for different corallites from a single corallum. Symbols for Section-intervals: □ 23-3 (Lawrence Quarry); n (number of coralla) = 1; ◇ 14-1 and 14-2 (Higginbotham Farm); n = 4; ○ 15-1 (Calumet); n = 1.

1.4 mm, with an average of 4.5 tabulae in 5 mm (Table 21).

Discussion.—These specimens show considerable variability in characters such as septal thickness, axial structure, thickness of stereozone, and growth habit. They may represent more than one species, but since the available specimens are fragmentary and few, it is not possible to make a definite determination. They are identified as *Palaeophyllum* sp.

Several other Late Ordovician and earliest Silurian species of *Palaeophyllum* have cateniform to fasciculate colony growth habits, and corallite diameters and number of major septa comparable to those of *Palaeophyllum* sp. Among these, the most similar is *Palaeophyllum vaurealense* Twenhofel (1928, pp. 122, 123, pl. 4, fig. 1) from the Vauréal Formation of Anticosti Island, Québec (Upper Ordovician, Richmondian; Barnes, 1988, fig. 2), also described and illustrated by Bolton (1979, p. 7, pl. 1.3, figs. 1–10). *Palaeophyllum vaurealense* has corallite diameters of about 2.5–4.4 mm, 13–16 major septa, commonly well-developed minor septa, stereozones of variable thickness, and colony growth habits ranging from sub-cerioid through cateniform to fasciculate. It differs from *Palaeophyllum* sp. by having much more slender major septa that more commonly extend to the corallite axis.

Species of similar character from western North America include: *Palaeophyllum gracile* Flower (1961, pp. 89, 90, pl. 46, pl. 47, figs. 1–8) from the Second Value Formation in Texas (Upper Ordovician, middle Edenian–lowermost Maysvillian; Sweet, 1979, fig. 4), also described and illustrated by Pandolfi (1985, p. 37, pl. 15, fig. 1, pl. 23, figs. 1, 2) from the Upper Ordovician Lost Canyon Member of the Ely Springs Dolomite in the Northern Egan Range, Nevada, and by Gierlowski and Langenheim (1985, p. 7, pl. 1, figs. 1–4) from the Horseshoe Mountain Member of the Bighorn Dolomite in Wyoming (Richmondian); *Palaeophyllum raduguini* Nelson (1963, p. 32, pl. 6, fig. 7) from the Caution Creek and Chasm Creek formations of the Hudson Bay Lowland, northern Manitoba (both Richmondian; see Elias, 1991, fig. 3), also described and illustrated by Bolton (in Bolton and Nowlan, 1979, p. 6, pl. 3, figs. 1, 2, 5) from an outlier north of Aberdeen Lake, Northwest Territories (upper Maysvillian–Richmondian); *Palaeophyllum sinclairi* Caramanica (1992, pp. 75–79, fig. 19, pl. 6, figs. 1–5) from the Bighorn Dolomite in Wyoming (Richmondian); and *Palaeophyllum pasense pasense* Stearn (1956, pp. 89, 90, pl. 16, fig. 7) from the Stonewall Formation in southern Manitoba (uppermost Ordovician to lowermost Silurian, Lower Llandovery, lower Rhuddanian; Sweet, 1979, p. 54, fig. 4; Johnson and Lescinsky, 1986, fig. 2). Our *Palaeophyllum* sp. differs from all of these by having generally thicker major septa, longer minor septa, and thicker stereozones.

Palaeophyllum minimum Yü (1960, pp. 80, 96, pl. 1, figs. 12, 13), from the Upper Ordovician of China, has corallites with diameters of about 3.0–3.5 mm and about 15–19 major septa, but is distinguished from *Palaeophyllum* sp. by having flat tabulae and apparently shorter major septa.

Occurrences.—Uppermost Ordovician (Gamachian): lower Keel Formation, south-central Oklahoma. Lowermost Silurian (?; Lower Llandovery?, lower Rhuddanian?): Kissenger Limestone Member, Bryant Knob Formation, northeastern Missouri.

Material described above.—Six specimens: USNM 485954, site 23i, interval 23-3, Keel Formation, Section 23 (Lawrence Quarry), Pontotoc County, Oklahoma; USNM 485955, interval 15-1, Kissenger Limestone Member, Bryant Knob Formation, Section 15 (Calumet), Pike County, Missouri; USNM 485956, interval 14-1, USNM 485957–485959, interval 14-2, Kissenger Limestone Member, Bryant Knob Formation, Section 14 (Higginbotham Farm), Pike County, Missouri.

Family **PYCNOSTYLIDAE** Stumm in Shrock and Twenhofel, 1953

Genus **PYCNOSTYLUS** Whiteaves, 1884

Pycnostylus Whiteaves, 1884, p. 2.

Type species.—By subsequent designation (Miller, 1889, p. 202): *Pycnostylus guelphensis* Whiteaves (1884, pp. 3, 4, pl. 1, figs. 1, 1a, 1b); Guelph Formation (Upper Silurian), Ontario.

Diagnosis.—"Fasciculate, increase peripheral, commonly four offsets simulating axial quadripartite increase; corallites with very narrow peripheral stereozone; septa amplexoid, peripheral continuous part very short; no dissepiments; tabulae complete, horizontal" (Hill, 1981, p. F140).

Pycnostylus species A

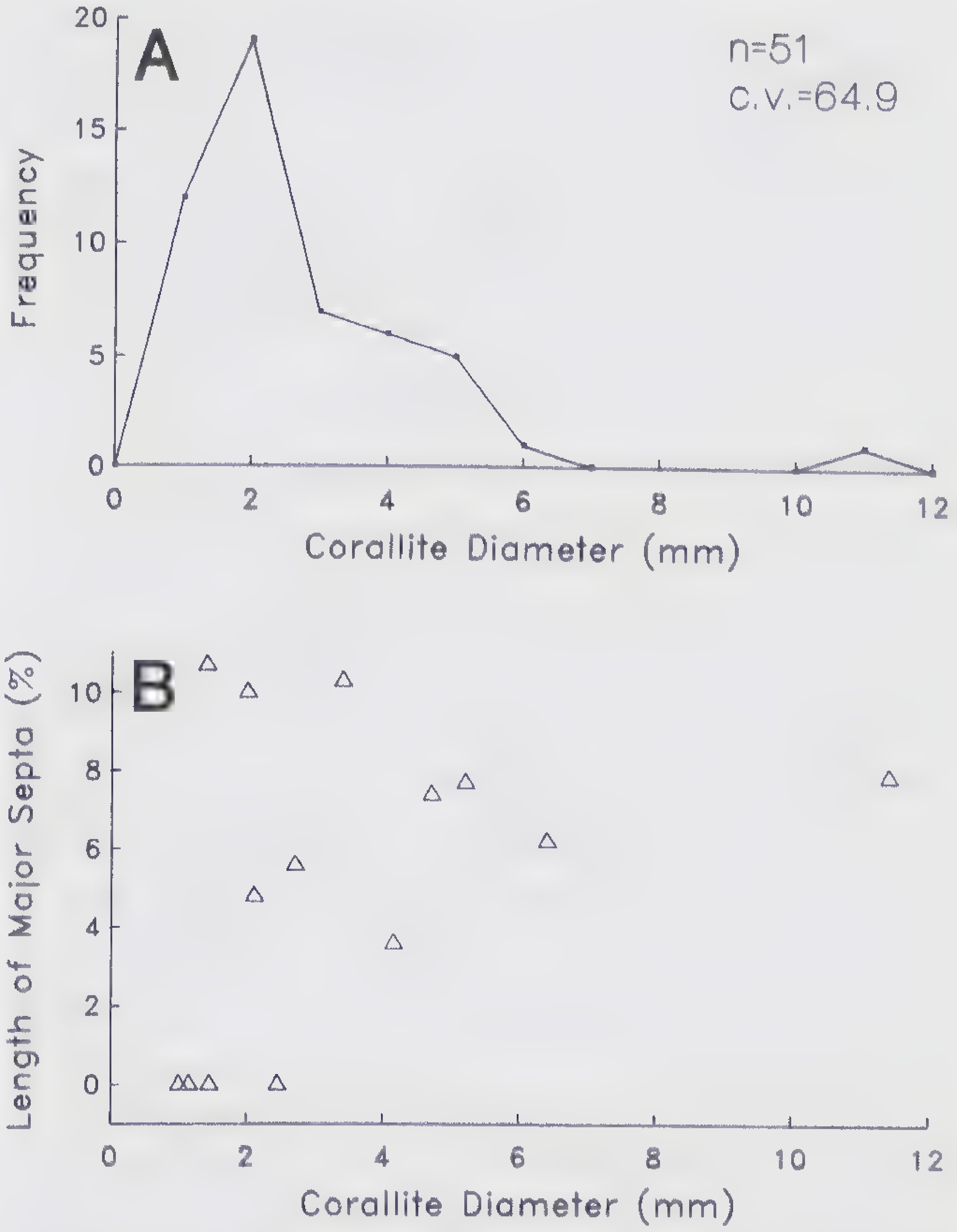
Plate 21, figures 15–25

Description.—All material is fragmentary, so it is not possible to determine larger scale aspects of colony form. Growth habits of coralla are apparently fasciculate.

Corallites are subcylindrical to cylindrical. In transverse section and on external surfaces, they are smooth or have variably developed septal grooves and interseptal ridges (Pl. 21, figs. 16, 17, 23, 25). Corallite diameters are variable, 0.55–11.40 mm but mostly 1–5 mm (Table 22; Text-fig. 34A). Corallites have lengths to more than 35 mm: in longitudinal section they are parallel-sided or slightly conical; walls may be straight

Table 22.—Biometric data for *Pycnostylus* sp. A from the east-central United States. *CoD* = corallite diameter, *WT* = wall thickness, *LS* = length of major septa, *Ta5* = number of tabulae in 5 mm; s.d. = standard deviation, c.v. = coefficient of variation.

	parameters			
data	*CoD*	*WT*	*LS*	*Ta5*
mean	2.76 mm	0.076 mm	5%	2.2
s.d.	1.79 mm	0.027 mm	4%	1.0
c.v.	64.9	35.5	80.3	45.5
minimum	0.55 mm	0.050 mm	0%	1
maximum	11.40 mm	0.175 mm	11%	4
no. of corallites studied	51	41	14	17



Text-figure 34.—Intraspecific variation in *Pycnostylus* sp. A; Section-interval 32-1b (Thomson East). **A**, Corallite size-frequency distribution for all measured corallites; n = number of corallites, c.v. = coefficient of variation. **B**, Relationship between length of major septa as a percentage of corallite radius and corallite diameter, for 14 corallites; each data point represents an individual corallite.

or wavy (Pl. 21, figs. 19, 24). A colonial mode of growth is demonstrated by short to moderately long connections between corallites at or near their bases, which may represent locations of increase (Pl. 21, fig. 20). Connections between more mature parts of corallites are rare or absent.

Corallite walls are thin, 0.050–0.175 mm (Table 22); poor preservation prevents differentiation of the epitheca and stereozone. Septa are lamellar; a single septum can be amplexoid (Pl. 21, figs. 23, 25) or can form a ridge showing relatively constant development (Pl. 21, fig. 18). Major septa are moderately thick and short, with lengths up to 11% of the corallite radius (Table 22). In a transversely sectioned corallite, all major septa are of about the same length (Pl. 21, figs. 16, 23). Minor septa are recognizable where they rarely extend beyond the stereozone. They are short, up to about 3% of the corallite radius, and are thinner than major septa (Pl. 21, fig. 17). Occurrence and abundance of septa generally increase with corallite diameter, with up to 28 major septa in the largest corallites. Septa are absent in all corallites with diameters less than 1 mm; their reduction in transverse sections of some larger individuals (Text-fig. 33B) may be due to the amplexoid nature of septa.

Tabulae are of moderate thickness, commonly concave, convex, or irregular; sometimes incomplete (Pl. 21, figs. 19, 24). They are broadly spaced, averaging about two in 5 mm (Table 22).

Discussion.—These specimens are identified as *Pycnostylus* sp. A. A specific name is not assigned because the material is preserved as dissociated corallites in channel-fill beds, and the degree of breakage prevents assessment of spatial relationships between corallites. This species is the oldest known representative of this Silurian genus, but it is morphologically similar to the other species, which are of early Early Silurian (latest Llandovery) to early Late Silurian (Ludlow) age. *Pycnostylus* sp. A most closely resembles the type species, *Pycnostylus guelphensis* Whiteaves (1884, pp. 3, 4, pl. 1, figs. 1, 1a, 1b), from the Guelph Formation of southwestern Ontario (Ludlow; Winder and Sanford, 1972, fig. 2). The latter species has corallites similar in size to those of *Pycnostylus* sp. A, with diameters of about 3–7 mm, and continuous lamellar septa. Based on Whiteaves' illustrations, it may differ from *Pycnostylus* sp. A by having a higher frequency of corallite increase.

Pycnostylus guelphensis, as described and illustrated by Stearn (1956, p. 82, pl. 8, fig. 7) from the Cedar Lake Formation of southern Manitoba (Upper Llandovery, Telychian, to upper Lower Silurian, Wenlock; Johnson and Lescinsky, 1986, fig. 2), is also very similar to *Pycnostylus* sp. A. Stearn's corals have continuous lamellar or slightly amplexoid septa, occurring in cylindrical corallites that are not joined together above the point of increase. Although the mean corallite diameter given by Stearn (5.6 mm) is significantly larger than that of *Pycnostylus* sp. A, this is apparently based only on corallites that he considered to be mature, and it does fall within the range for our material.

Occurrence.—Lowermost Silurian (Lower Llandovery, lower Rhuddanian): lower Mosalem Formation, northwestern Illinois.

Material described above.—Eight specimens (each includes several dissociated corallites): USNM 485960–485967, interval 32-1b, Mosalem Formation, Section 32 (Thomson East), Carroll County, Illinois.

APPENDIX

Stratigraphic Sections

Introduction

The locations of stratigraphic sections are designated using United States Geological Survey topographic quadrangle maps (1:24,000 scale). Precise coordinates following the map name are measured in mm first east and then north from the southwest corner of the map. Descriptions of the sections and lists of fossils are contained in the references cited under each entry.

The six outcrop areas (A–F) are outlined in Text-figure 1A (detail map, foldout inside front cover). All the numbered sections (but not Gale Section) were examined during this study. Locations of sections, positions of numbered collection intervals, and stratigraphic and paleontologic data are shown in Text-figures 2–7. Collection intervals are numbered as follows: Section-interval (*e.g.*, 23-2 is Section 23, interval 2).

A. South-central Oklahoma

21 (Rock Crossing).—Overbrook, Oklahoma Quadrangle: 310 mm E, 348 mm N; SE¼ NE¼ SW¼ sec. 35, T 5 S, R 1 E. Exposure on west bank of Hickory Creek, east side of road, 0.15 km south of bridge, Carter County, Oklahoma (Amsden, 1960, sec. Ca11, pp. 208–210, panel 1; Barrick, 1986, sec. Ca11, fig. 39; McAuley and Elias, 1990, sec. 21, pp. 8, 53, fig. 2; Elias, 1992, p. 122, fig. 2). Collection from Section-interval 21-1b made in lens of bioclastic limestone.

22 (Cedar Village).—Turner Falls, Oklahoma Quadrangle: 437 mm E, 326 mm N; SE¼ NE¼ NW¼ sec. 30, T 1 S, R 2 E. Cut on west side of U.S. Route 77, 0.5 km south of junction with Interstate Route 35, just north of Cedar Village, Murray County, Oklahoma (section enlarged and improved since description by Amsden, 1960, sec. M17, pp. 256–258, panel 1; Amsden in Ham, 1973, fig. 35; Barrick, 1986, sec. M17, fig. 39; Fay, 1988, p. 188, fig. 2c; Fay, 1989, marker no. 14, pp. 7, 47, pl. 1; Barrick *et al.*, 1990, p. 5, fig. 2; McAuley and Elias, 1990, sec. 22, pp. 8, 53).

23 (Lawrence Quarry).—Ahloso, Oklahoma Quadrangle. Site 23i: 95 mm E, 301 mm N; NW¼ SE¼ NE¼ sec. 36, T 3 N, R 5 E. Site 23ii: 95 mm E, 290 mm N; SW¼ SE¼ NE¼ sec. 36, T 3 N, R 5 E. Site 23iii: 95 mm E, 288 mm N; SW¼ SE¼ NE¼ sec. 36, T 3 N, R 5 E. Site 23iv: 94 mm E, 286 mm N; NW¼ NE¼ SE¼ sec. 36, T 3 N, R 5 E. East side of Ideal Cement Company quarry at Lawrence, Pontotoc County, Oklahoma; type section of Keel Formation and Ideal Quarry Member (Amsden, 1960, pl. 1, figs. 1, 2, panel 2, pl. A; Amsden, 1974, loc. P22, p. 87; Amsden, 1986, figs. 5, 6, 15; Barrick, 1986, sec. AQL, fig. 39; McAuley and Elias, 1990, sec. 23, pp. 8, 53, fig. 2; Elias, 1992, p. 122, fig. 2).

24 (Coal Creek).—Harden City, Oklahoma Quadrangle: 253 mm E, 208 mm N; NW¼ SE¼ NW¼ sec. 22, T 1 N, R 7 E. Exposure on north bank of Coal Creek, 0.4 km east of Gobbler Knob, Pontotoc County, Oklahoma (Amsden, 1957, fig. 5; Amsden, 1960, sec. P9, pp. 279–282, panel 1; Amsden, 1961, fig. 25; Amsden, 1986, fig. 13; Barrick, 1986, sec. P9, fig. 39; McAuley and Elias, 1990, sec. 24, pp. 8, 53, fig. 2; Elias, 1992, p. 122, fig. 2).

25 (Hunton).—Wapanucka North, Oklahoma Quadrangle: 14 mm E, 519 mm N; NE¼ SE¼ NE¼ sec. 7, T 1 S, R 8 E. Exposure 0.5 km south of northeast corner of section, Coal County, Oklahoma; base of type section of Hunton Group (Amsden, 1960, sec. C1, pp. 182, 184–188, panel 2, pl. B; McAuley and Elias, 1990, sec. 25, p. 53, fig. 2).

35 (Henry House Falls).—Springer, Oklahoma Quadrangle: 65 mm E, 464 mm N; SW¼ NE¼ SE¼ sec. 30, T 2 S, R 1 E. Exposure on west side of Henry House Creek at upper rim of Henry House Falls, Carter County, Oklahoma (Amsden, 1960, sec. Ca1 (2), pp. 190–195, panel 1; Elias, 1992, p. 122, fig. 2).

B. Western north-central Arkansas

33 (Buffalo River).—Marshall, Arkansas Quadrangle: 35 mm E, 512 mm N; NE¼ SW¼ and NW¼ SE¼ sec. 36, T 16 N, R 17 W. Exposure on north bank of Buffalo River, 0.5 km east of bridge on U.S. Route 65, Searcy County, Arkansas (Lemastus, 1979, pp. 86–88, pl. 1; Craig, 1984, p. 11, fig. 2; Craig, 1988, loc. 3, pp. 212, 213, figs. 3, 4; McAuley and Elias, 1990, sec. 33, pp. 10, 53, fig. 3).

C. Southern Illinois and southeastern Missouri

19 (New Wells).—Neelys Landing, Missouri–Illinois Quadrangle: 24 mm E, 254 mm N; NW¼ SW¼ SW¼ sec. 9, T 33 N, R 13 E. Exposure along channel and east bank of Blue Shawnee Creek, 0.5 km east of New Wells, Cape Girardeau County, Missouri (Amsden, 1974, loc. U, pp. 21, 22, 87, fig. 17; Thompson and Satterfield, 1975, sec. 4, p. 79, fig. 9; Elias, 1982, loc. 20b, p. 39, fig. 21; Amsden, 1986, pp. 32–34; McAuley and Elias, 1990, sec. 19, pp. 10, 11, fig. 4).

20 (Short Farm).—Cape Girardeau NE, Missouri Quadrangle: 44 mm E, 276 mm N; SE¼ NE¼ SW¼ sec. 21, T 32 N, R 13 E. Exposure along creek channel just east of barn, 0.25 km east of State Route W, Cape Girardeau County, Missouri; type section of Leemon Formation (Amsden, 1974, loc. K, pp. 19, 85, 86, fig. 16; Thompson and Satterfield, 1975, sec. 3, fig. 7; Elias, 1982, loc. 20a, p. 39, fig. 21; Amsden, 1986, pp. 31, 32, fig. 25; McAuley and Elias, 1990, sec. 20, pp. 10–12, 53, 54, fig. 4). Collections for Section-intervals 20-3 and 20-6 made from loose blocks.

31 (Thebes North).—Thebes, Illinois–Missouri Quadrangle: 157 mm E, 506 mm N; SE¼ SE¼ sec. 5, T 15 S, R 3 W. Exposure on east bank of Mississippi River, 1.5 km southwest of Gale and 1.8 km north of Thebes, Alexander County, Illinois (Savage, 1910, pp. 331, 332, pl. 36, fig. a; Savage, 1913, pp. 20, 21; Savage, 1917, pp. 77–79; Weller, 1940, pp. 8–10; Pryor and Ross, 1962, pp. 7–10, fig. 3; Satterfield, 1971, p. 266, fig. 1; Amsden, 1974, loc. M, pp. 23, 24, 86; Thompson and Satterfield, 1975, sec. 1, pp. 77, 78, fig. 8; Amsden, 1986, pp. 29, 30, fig. 22; McAuley and Elias, 1990, sec. 31, pp. 10–12, 53, fig. 4).

Gale Section.—Thebes, Illinois–Missouri Quadrangle: precise coordinates unknown; NE¼ sec. 4, T 15 S, R 3 W. Abandoned quarry 0.4 km southeast of Gale, Alexander County, Illinois (Savage, 1910, pp. 332, 333, pl. 37, fig. a; Savage, 1913, pp. 21, 22; Savage, 1917, p. 79; McAuley and Elias, 1990, pp. 12, 53, fig. 4) (for cut along State Route 3 in same vicinity, see Weller, 1940, pp. 8–10; Pryor and Ross, 1962, pp. 7–10, fig. 3; Cote *et al.*, 1968, stop 1, pp. 7–10, figs. 6, 7; Amsden, 1974, loc. L, pp. 23, 24, 86; Amsden, 1986, p. 30).

D. West-central Illinois and northeastern Missouri

13 (Bowling Green).—Bowling Green, Missouri Quadrangle: 197 mm E, 497 mm N; NW¼ NW¼ sec. 24, T 53 N, R 3 W. Cut on north side of U.S. Route 54, 1.5 km northeast of junction with U.S. Route 61, Pike County, Missouri; reference section of Cyrene Formation and Bowling Green Dolomite (Koenig *et al.,* 1961, fig. 15; Amsden, 1974, loc. D, p. 84, figs. 4, 7; Thompson and Satterfield, 1975, sec. 8, pp. 96, 99, fig. 11; Elias, 1982, Bowling Green sec., fig. 21; Amsden, 1986, sec. D, figs. 31, 34; McAuley and Elias, 1990, sec. 13, pp. 14, 54, fig. 5; Elias, 1992, p. 122, fig. 3).

14 (Higginbotham Farm).—Cyrene, Missouri Quadrangle: 391 mm E, 418 mm N, and 392 mm E, 424 mm N; W½ NW¼ NE¼ sec. 28, T 53 N, R 1 W. Exposures north (Section-interval 14-1) and south (Section-interval 14-2) of abandoned house (only the foundation remains), just east of State Route D, Pike County, Missouri (Laswell, 1957, sec. 5, p. 20; Amsden, 1974, loc. A, p. 83, fig. 4; Thompson and Satterfield, 1975, p. 93, fig. 16; McAuley and Elias, 1990, sec. 14, p. 54, fig. 5).

15 (Calumet).—Cyrene, Missouri Quadrangle: 415 mm E, 432 mm N, to 404 mm E, 434 mm N; S½ SE¼ sec. 21, T 53 N, R 1 W. Abandoned quarry east of Stark Cemetery, 0.5 km east of State Route D, Pike County, Missouri (Thompson and Satterfield, 1975, sec. 5, p. 93, figs. 15, 16; McAuley and Elias, 1990, sec. 15, p. 54, fig. 5).

16 (Clinton Spring).—Louisiana, Missouri–Illinois Quadrangle: 312 mm E, 312 mm N; SW¼ NE¼ NW¼ sec. 20, T 54 N, R 1 W. Exposure just west of Clinton Spring on west side of State Route 79, southern edge of Louisiana, Pike County, Missouri; type section of Noix Limestone (Laswell, 1957, sec. 4, pp. 18, 19; Koenig *et al.,* 1961, stop 8, p. 34, figs. 21, 22; Birkhead, 1967, loc. I, fig. 4; Amsden, 1974, loc. B, p. 83, fig. 4; Thompson and Satterfield, 1975, sec. 7, p. 89, fig. 12; Elias, 1982, loc. 21b, p. 40, fig. 21; Amsden, 1986, fig. 34, sec. B; McAuley and Elias, 1990, sec. 16, pp. 14, 15, 54, fig. 5).

17 (Clarksville).—Clarksville, Missouri–Illinois and Pleasant Hill West, Illinois–Missouri quadrangles: 333 mm E, 564 mm N (Clarksville) to 313 mm E, 1 mm N (Pleasant Hill West); SW¼ sec. 9, T 53 N, R 1 E. Cut on west side of State Route 79, northern edge of Clarksville, Pike County, Missouri (Amsden, 1974, loc. E, p. 84, figs. 4–6; Thompson and Satterfield, 1975, sec. 6, pp. 99, 100, sec. 6, fig. 13; Elias, 1982, loc. 21a, p. 40; McCracken and Barnes, 1982, fig. 2; Amsden, 1986, sec. E, figs. 33, 34; McAuley and Elias, 1990, sec. 17, pp. 14–16, 54, figs. 5, 6).

18 (Kissenger).—Annada, Missouri–Illinois Quadrangle: 15 mm E, 312 mm N; SW¼ sec. 35 (projected), T 53 N, R 1 E. Cut on west side of State Route 79, just west of Kissenger Hill and south of spring; type section of Bryant Knob Formation and Kissenger Limestone Member (Amsden, 1974, loc. F, pp. 84, 85, fig. 4; Thompson and Satterfield, 1975, sec. 11, pp. 97–100, fig. 14; Amsden, 1986, sec. F, figs. 32, 34; McAuley and Elias, 1990, sec. 18, pp. 14–16, 54, fig. 5).

36 (Indian Creek).—Hamburg, Illinois–Missouri Quadrangle: 183 mm E, 306 mm N; NW¼ NW¼ NE¼ sec. 13, T 10 S, R 3 W. North- and west-facing exposures just south of Indian Creek and just east of County Route 2, 4.6 km south-southeast of Hamburg, Calhoun County, Illinois (Rubey, 1952, loc. 6, pp. 25–27, 170; Amsden, 1974, loc. I, p. 85; Thompson and Satterfield, 1975, sec. 12, p. 106; Elias, 1992, p. 122, fig. 3). Collection for Section-interval 36-2a made from loose block.

E. Northeastern Illinois

3 (Garden Prairie).—Riley, Illinois Quadrangle: 179 mm E, 566 mm N; NE¼ SW¼ sec. 31, T 44 N, R 5 E. Abandoned quarry, 0.5 km south of U.S. Route 20, McHenry County, Illinois (Willman, 1973, pp. 12, 14; McAuley and Elias, 1990, sec. 3, pp. 18, 20, 54, fig. 7).

4 (Schweizer West).—Channahon, Illinois Quadrangle; 302 mm E, 418 mm N; SW¼ SE¼ sec. 35, T 35 N, R 9 E. Cuts on both sides of lower (western) railroad (Section-interval 4-2 on east side of tracks), southeast side of Des Plaines River valley, Will County, Illinois; type section of Wilhelmi Formation, and Schweizer and Birds (lower part) members (Ross, 1962, fig. 1; Willman, 1962, stop 4, p. 84; Willman, 1973, sec. 17, pp. 50, 51; Liebe and Rexroad, 1977, loc. 8, p. 854, fig. 1; Elias, 1982, Will Co. sec., fig. 21; McAuley and Elias, 1990, sec. 4, pp. 18–20, 54, fig. 7; Elias, 1992, p. 123, fig. 4).

5 (Schweizer North).—Channahon, Illinois Quadrangle: 354 mm E, 449 mm N; SW¼ SW¼ NE¼ sec. 36, T 35 N, R 9 E. Cut on southeast side of lower (western) railroad, and ravine from there to southeast side of upper (eastern) railroad, at new concrete culvert, southeast side of Des Plaines River valley, Will County, Illinois; type section of Birds Member (upper part) of Wilhelmi Formation, and Elwood Formation (Ross, 1962, fig. 1; Willman, 1973, sec. 16, p. 50; Liebe and Rexroad, 1977, loc. 7, p. 854, fig. 1; Elias, 1982, Will Co. sec., fig. 21; McAuley and Elias, 1990, sec. 5, pp. 18–20, 54, fig. 7).

6 (Plaines West).—Channahon, Illinois Quadrangle: 405 mm E, 491 mm N; NW¼ SE¼ SW¼ sec. 30, T 35 N, R 10 E. Cut on southeast side of lower (western) railroad, southeast side of Des Plaines River valley, Will County, Illinois; type section of Drummond, Offerman, and Troutman (lower part) members, Kankakee Formation (Ross, 1962, fig. 1; Willman, 1973, sec. 14, pp. 49, 50; Liebe and Rexroad, 1977, loc. 6, p. 854, fig. 1; Elias, 1982, Will Co. sec., fig. 21; McAuley and Elias, 1990, sec. 6, pp. 20, 54, fig. 7).

29 (Sears Pit).—Sycamore, Illinois Quadrangle: 347 mm E, 336 mm N; SE¼ NW¼ and SW¼ NE¼ sec. 15, T 40 N, R 5 E. Quarry southeast of intersection of Barber Greene Road and Airport Road, 4 km northeast of Cortland, De Kalb County, Illinois (Mikulic *et al.,* 1985, pp. 21–23, figs. 6, 7; McAuley and Elias, 1990, sec. 29, pp. 20, 54, fig. 7; Elias, 1992, p. 123, fig. 4). Collection for Section-interval 29-4 made from loose block.

34 (Belvidere South).—Belvidere South, Illinois Quadrangle: 63 mm E, 367 mm N; SE¼ SW¼ NW¼ sec. 14, T 43 N, R 3 E. Abandoned quarry 0.35 km east of Stone Quarry Road, 4 km south of Belvidere, Boone County, Illinois (vicinity of Savage, 1926, p. 518; McAuley and Elias, 1990, sec. 34, pp. 18, 20, 54, fig. 7).

37 (Essex).—Essex, Illinois Quadrangle: 363 mm E, 240 mm N; NW¼ SW¼ SW¼ sec. 12, T 31 N, R 9 E. Exposure on north bank of Horse Creek, 3.3 km east of Essex, Kankakee Co., Illinois (Savage, 1912, p. 100, pl. 7; Savage, 1913, pp. 28, 29; Savage, 1917, pp. 86, 87; Athy, 1928, pp. 38–41, figs. 11, 12; McAuley and Elias, 1990, pp. 18, 20). Collection for Section-interval 37-1 made from loose blocks.

F. Northwestern Illinois and eastern Iowa

8 (King).—Menominee, Illinois–Iowa Quadrangle: 120 mm E, 105 mm N, to 113 mm E, 133 mm N; E½ SE¼ sec. 27, T 88 N, R 3 E. Cut on east side of U.S. Route 52, just south of King, Dubuque County, Iowa; type section of Mosalem and Tete des Morts formations (Willman, 1973, sec. 22, p. 52; McAuley and Elias, 1990, sec. 8, pp. 21, 22, 55).

9 (Winston).—Hanover, Illinois Quadrangle: 41 mm E, 461 mm N; SE¼ SW¼ NE¼ sec. 11, T 27 N, R 1 E. Quarry on east side of road, 1.8 km north of eastern end of Winston railroad tunnel, Jo Daviess County, Illinois (Willman, 1973, sec. 34, p. 55; McAuley and Elias, 1990, sec. 9, pp. 22, 55, fig. 8).

10 (Lost Mound).—Green Island, Iowa–Illinois Quadrangle: 288 mm E, 412 mm N; SW¼ NW¼ SW¼ sec. 28, T 26 N, R 2 E. East side of quarry in east bluff of Mississippi River valley, 1.3 km northwest of Lost Mound, Jo Daviess County, Illinois (Willman, 1973, sec. 24, pp. 52, 53; McAuley and Elias, 1990, sec. 10, pp. 22, 54, fig. 8).

11 (Schapville).—Elizabeth, Illinois Quadrangle: 92 mm E, 558 mm N; NE¼ NE¼ sec. 1, T 27 N, R 2 E. Cut on east side of road, 3.2 km southwest of Schapville, Jo Daviess County, Illinois (Willman, 1973, sec. 30, p. 54; McAuley and Elias, 1990, sec. 11, pp. 22, 55).

12 (Stockton).—Kent, Illinois Quadrangle: 148 mm E, 359 mm N; SE¼ SW¼ SW¼ sec. 17, T 27 N, R 5 E. Abandoned quarry at north edge of ridge, just south of road, 4 km southeast of Stockton, Jo Daviess County, Illinois (Willman, 1973, sec. 32, p. 54; McAuley and Elias, 1990, sec. 12, pp. 22, 55).

26 (Bellevue).—Springbrook, Iowa–Illinois Quadrangle: 288 mm E, 559 mm N, to 262 mm E, 572 mm N; NE¼ sec. 19, T 86 N, R 5 E. Exposure along west side of U.S. Route 52 and south side of road in Bellevue State Park, Jackson County, Iowa (Whitlow and Brown, 1963, p. 13; Ross, 1964, p. 1107, fig. 1; Rose, 1967, stop 3, pp. 44, 45, figs. 20, 21; Anderson, 1983, fig. 5.6; Ludvigson and Witzke, 1988, pp. 236, 237, fig. 21; McAuley and Elias, 1990, sec. 26, pp. 22, 54, 55, fig. 8; Elias, 1992, p. 123, fig. 6).

30 (Thomson Northeast).—Thomson, Illinois Quadrangle: 207 mm E, 452 mm N; NW¼ NW¼ NE¼ sec. 20, T 23 N, R 4 E. Quarry at top of bluff west of Johnson Creek, 3 km northeast of Thomson, Carroll County, Illinois (vicinity of Savage, 1926, p. 527; McAuley and Elias, 1990, sec. 30, pp. 22, 54, fig. 8).

32 (Thomson East).—Thomson, Illinois Quadrangle: 270 mm E, 377 mm N; SE¼ NE¼ NW¼ sec. 28, T 23 N, R 4 E. Quarry on rise east of Johnson Creek, 4.5 km east of Thomson, Carroll County, Illinois (McAuley and Elias, 1990, sec. 32, pp. 22, 54, figs. 8, 9; Elias, 1992, p. 123, fig. 6).

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PLATES

Exterior views are of specimens coated with ammonium chloride. Transverse and longitudinal sections are photomicrographs of thin sections. For serial transverse sections, orientation of the specimen remains the same from one figure to the next. Longitudinal sections are oriented with the direction of growth toward the top of the plate.

EXPLANATION OF PLATE 1

Figure		Page
1–11.	***Propora thebesensis*** (Foerste, 1909)	45

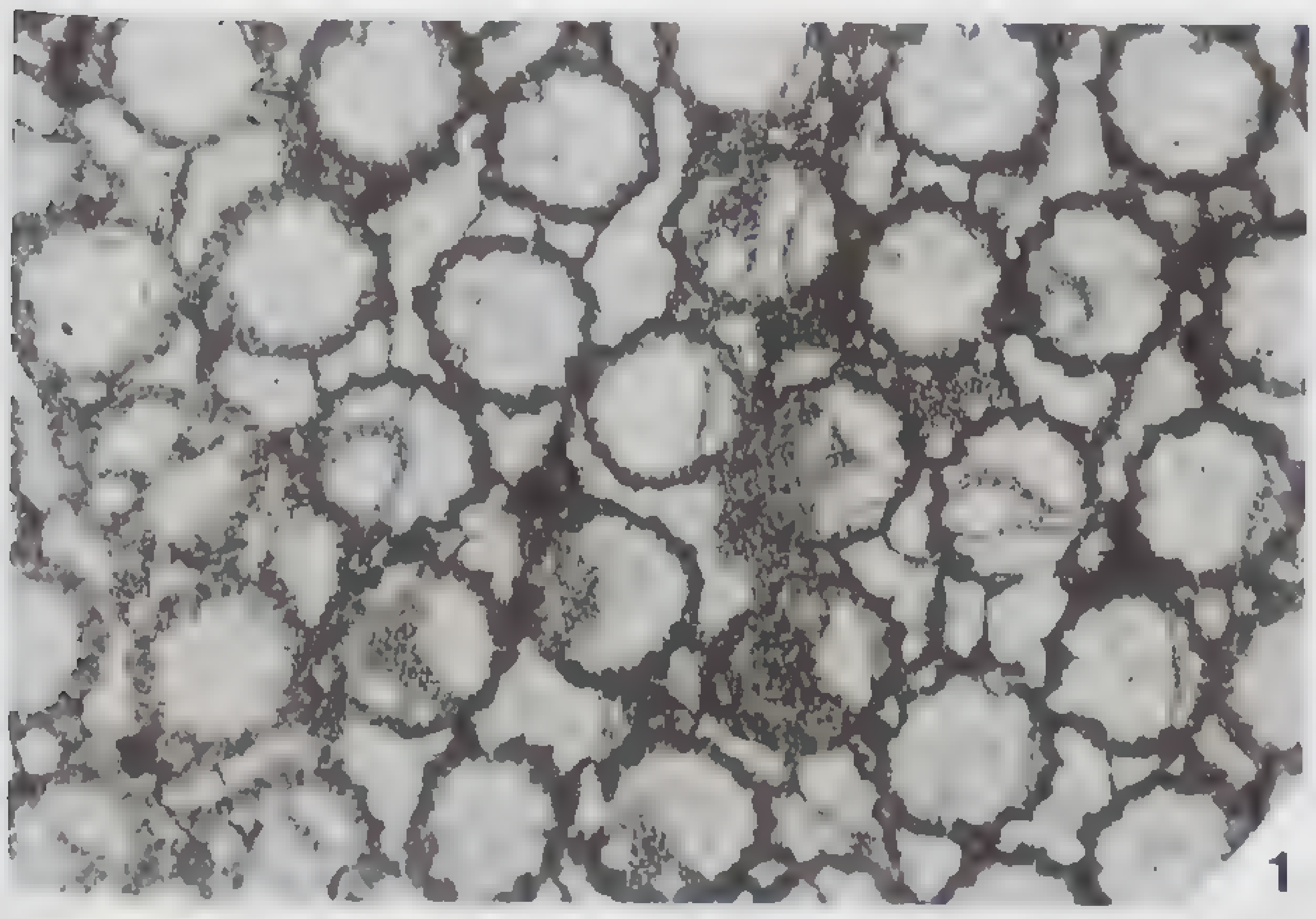
[1–11, *Brevilamnulella* beds, Keel Formation, Section-interval 23-2 (Lawrence Quarry) (1, 2, 4–9, site 23iii; 3, site 23i; 10, 11, site 23ii).]

1, 2. USNM 485706a: 1, transverse section, ×8; 2, longitudinal section, ×8.

3. USNM 485700: transverse section showing new tabularium, ×20.

4–9. USNM 458777: 4, transverse section showing new tabularium, ×20; 5, transverse section, ×8; 6, 7, transverse sections, ×40; 8, longitudinal section showing growth around crinoid grain, ×8; 9, longitudinal oblique section of a corallite, showing trabeculae, ×40.

10, 11. USNM 485703: 10, transverse section, ×8; 11, longitudinal section, ×8.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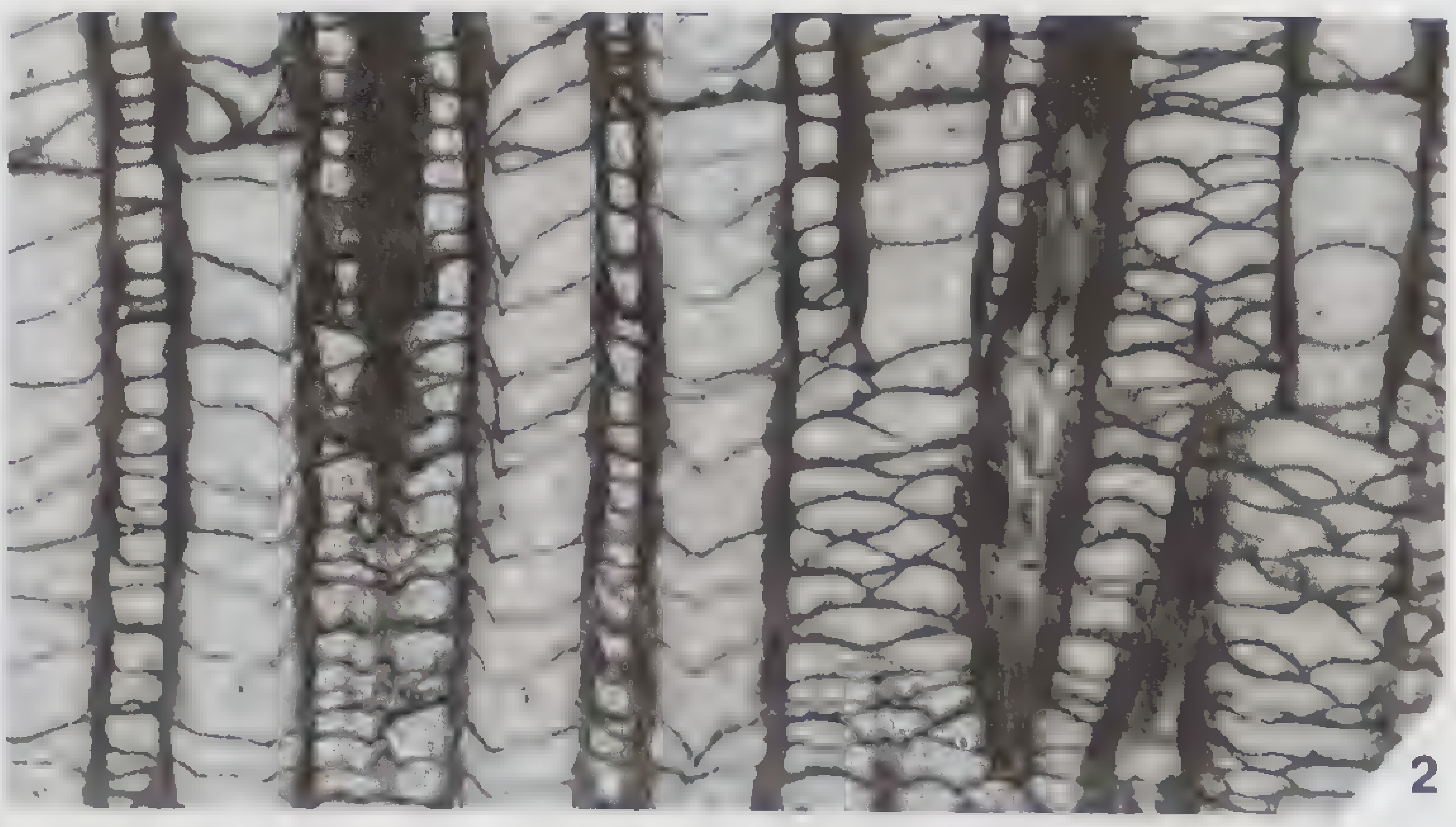
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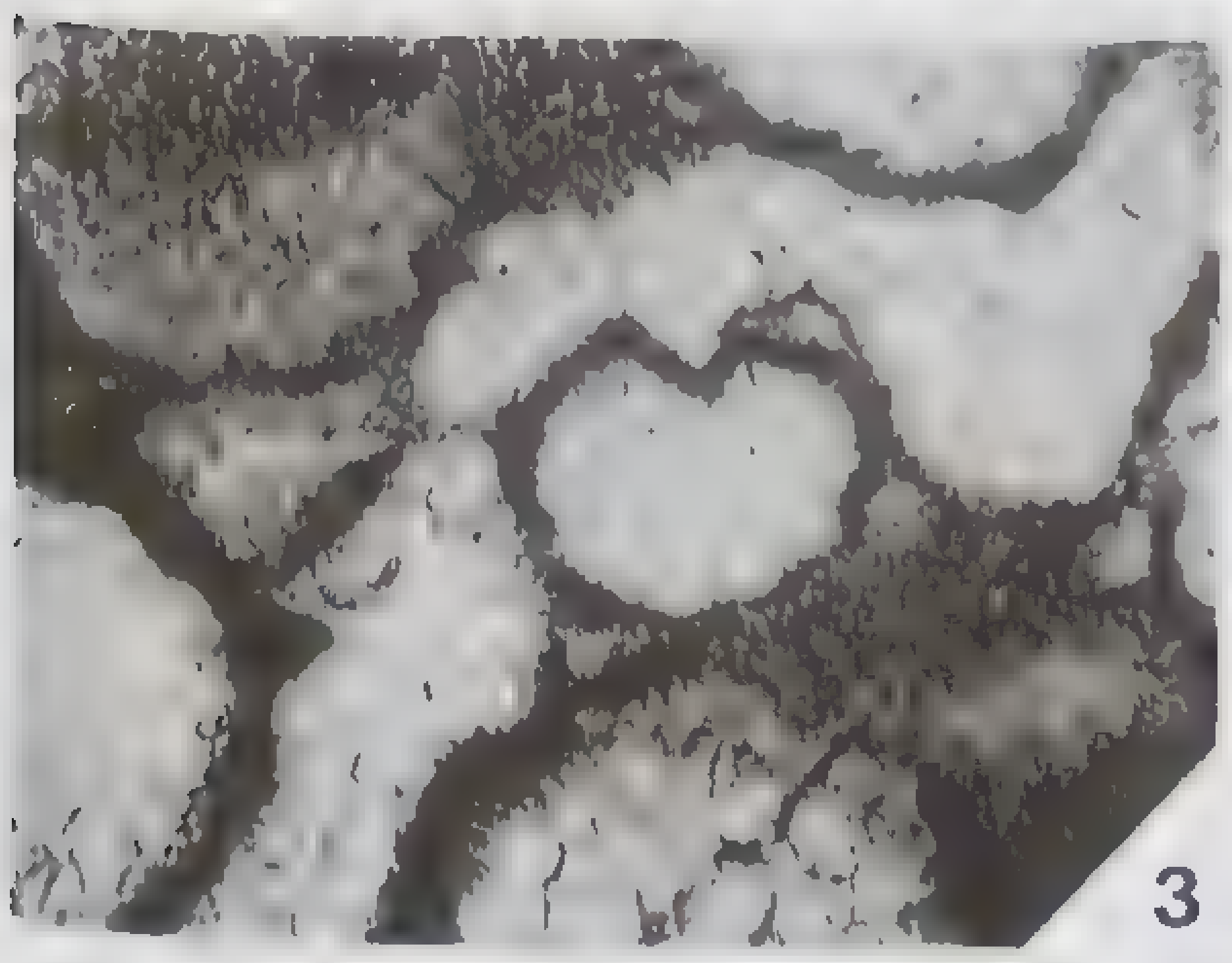
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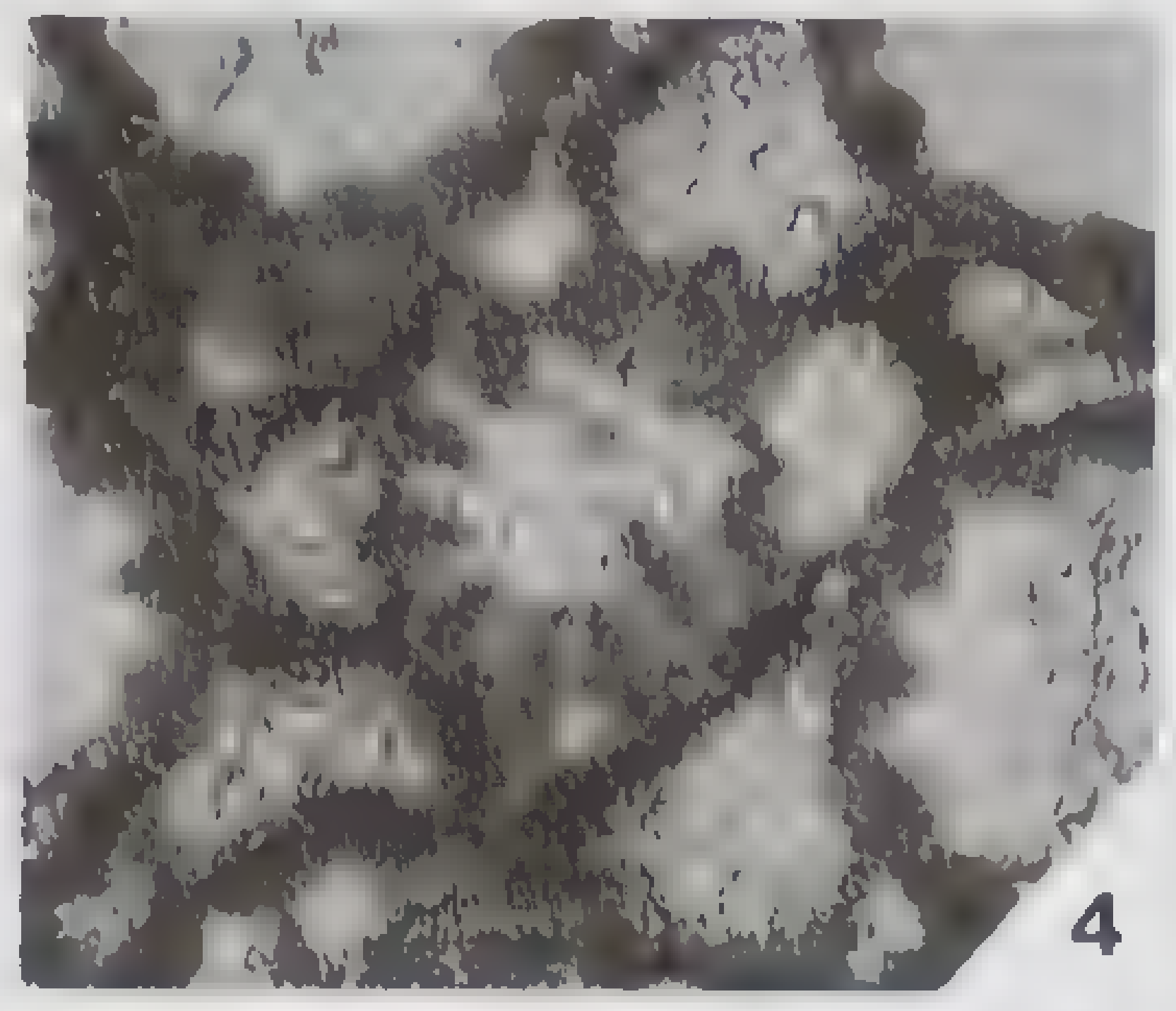
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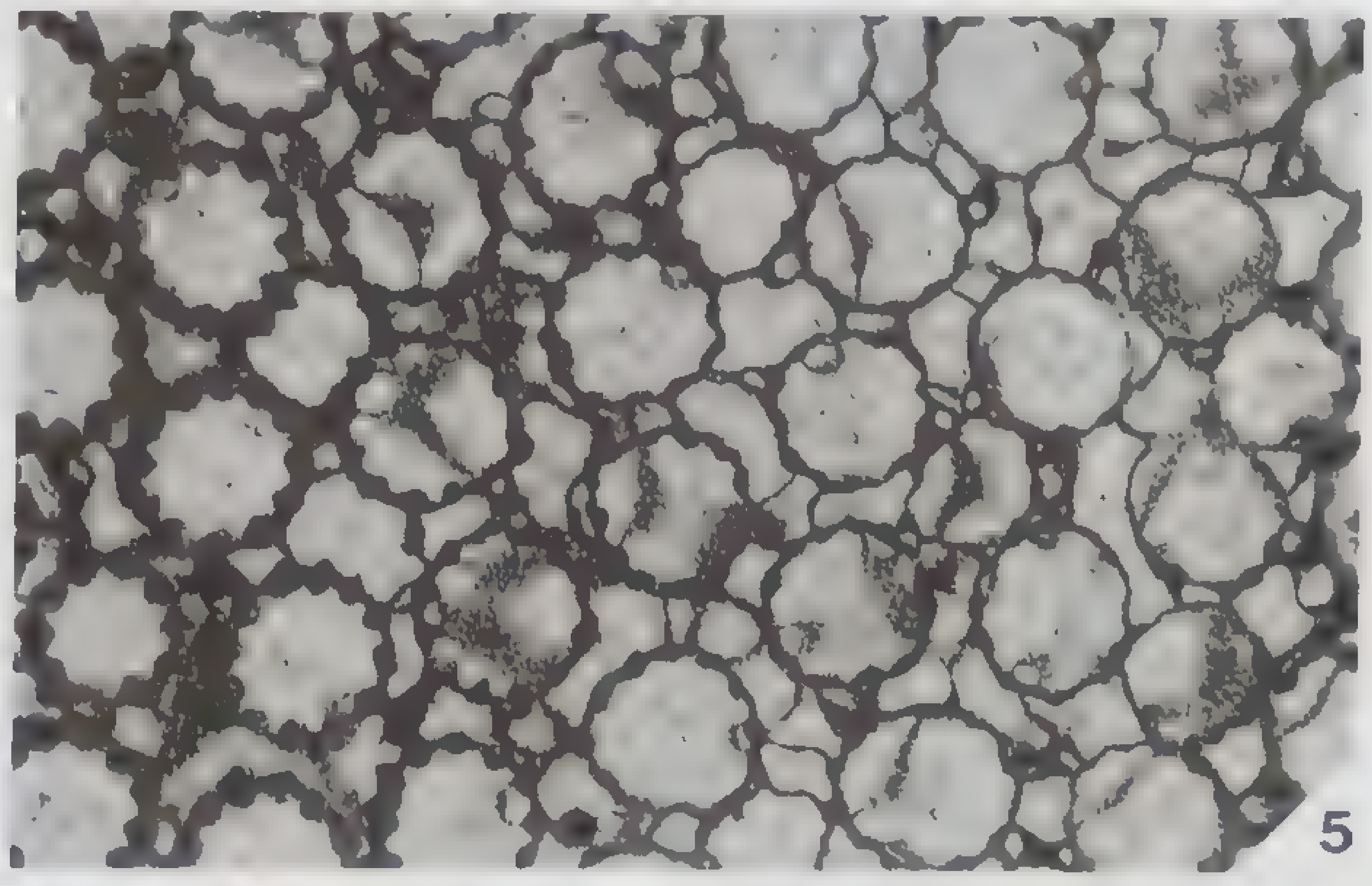
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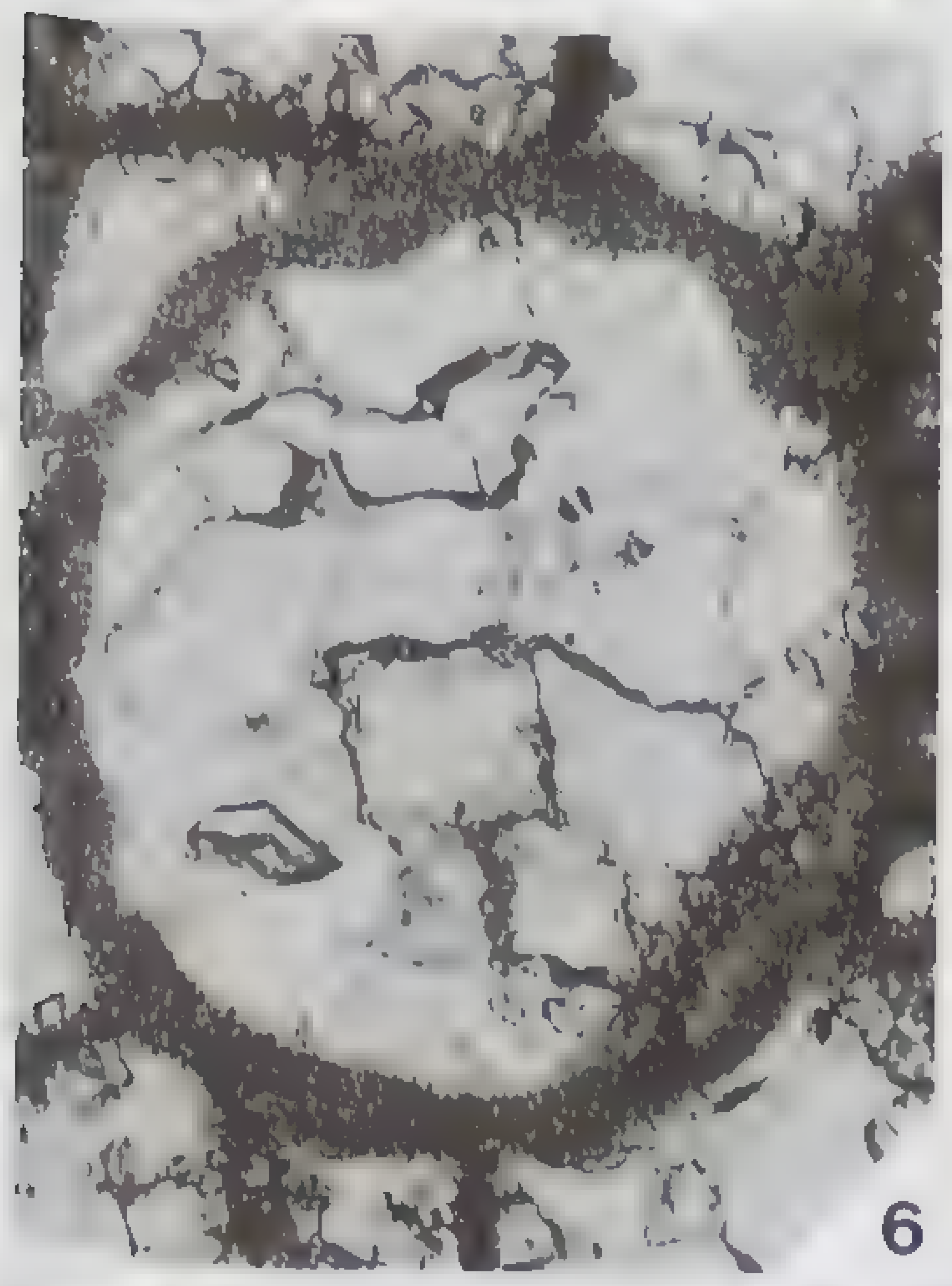
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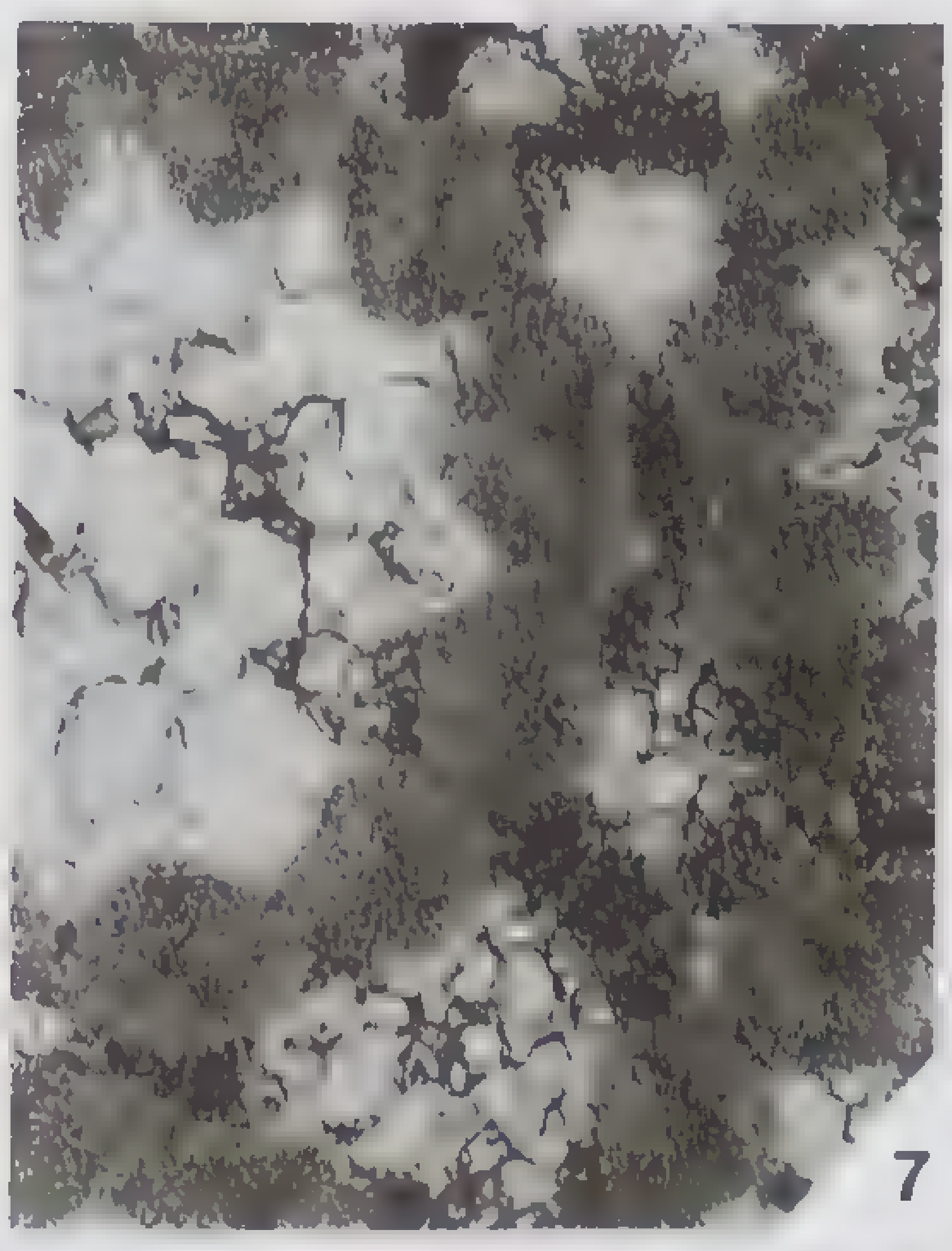
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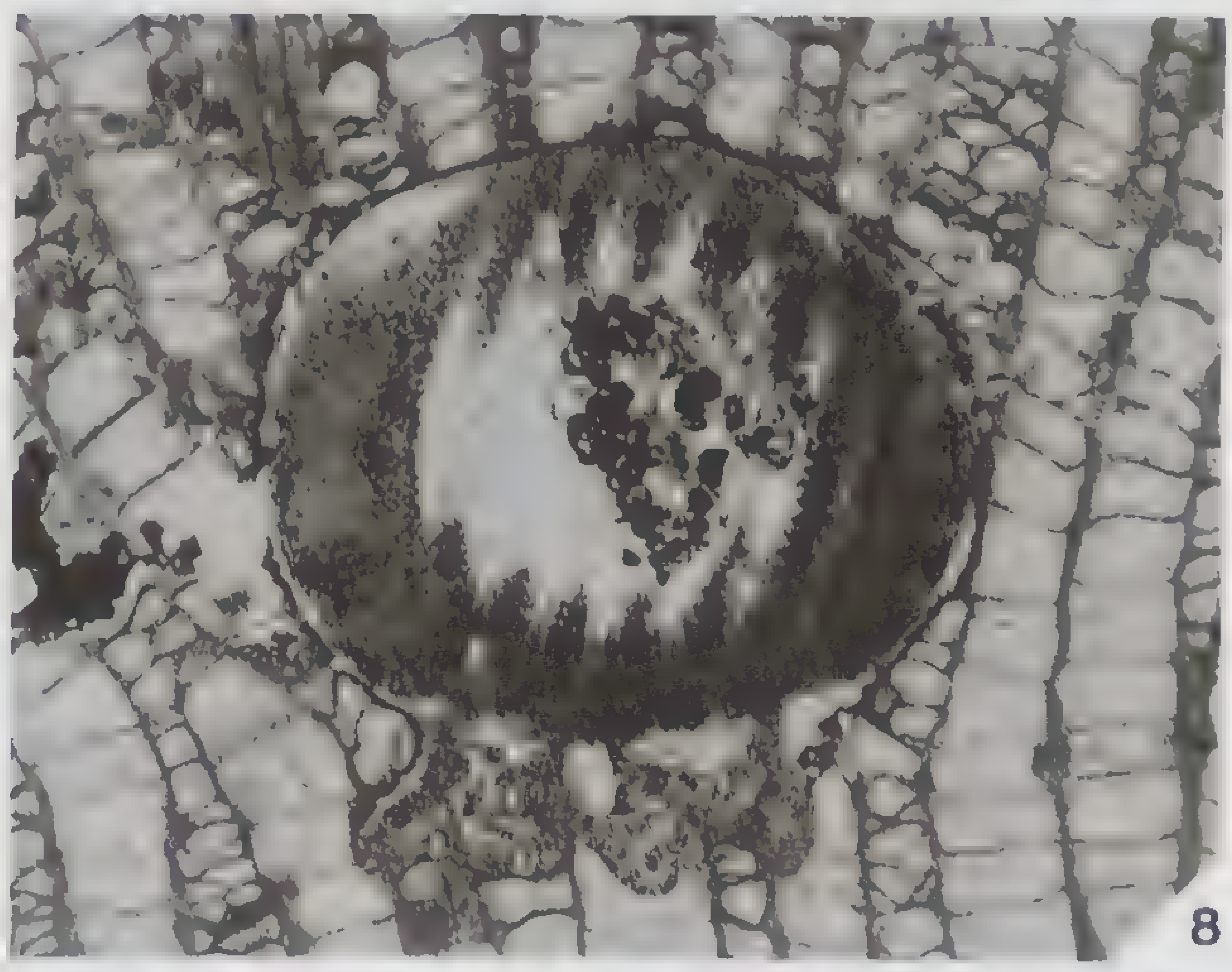
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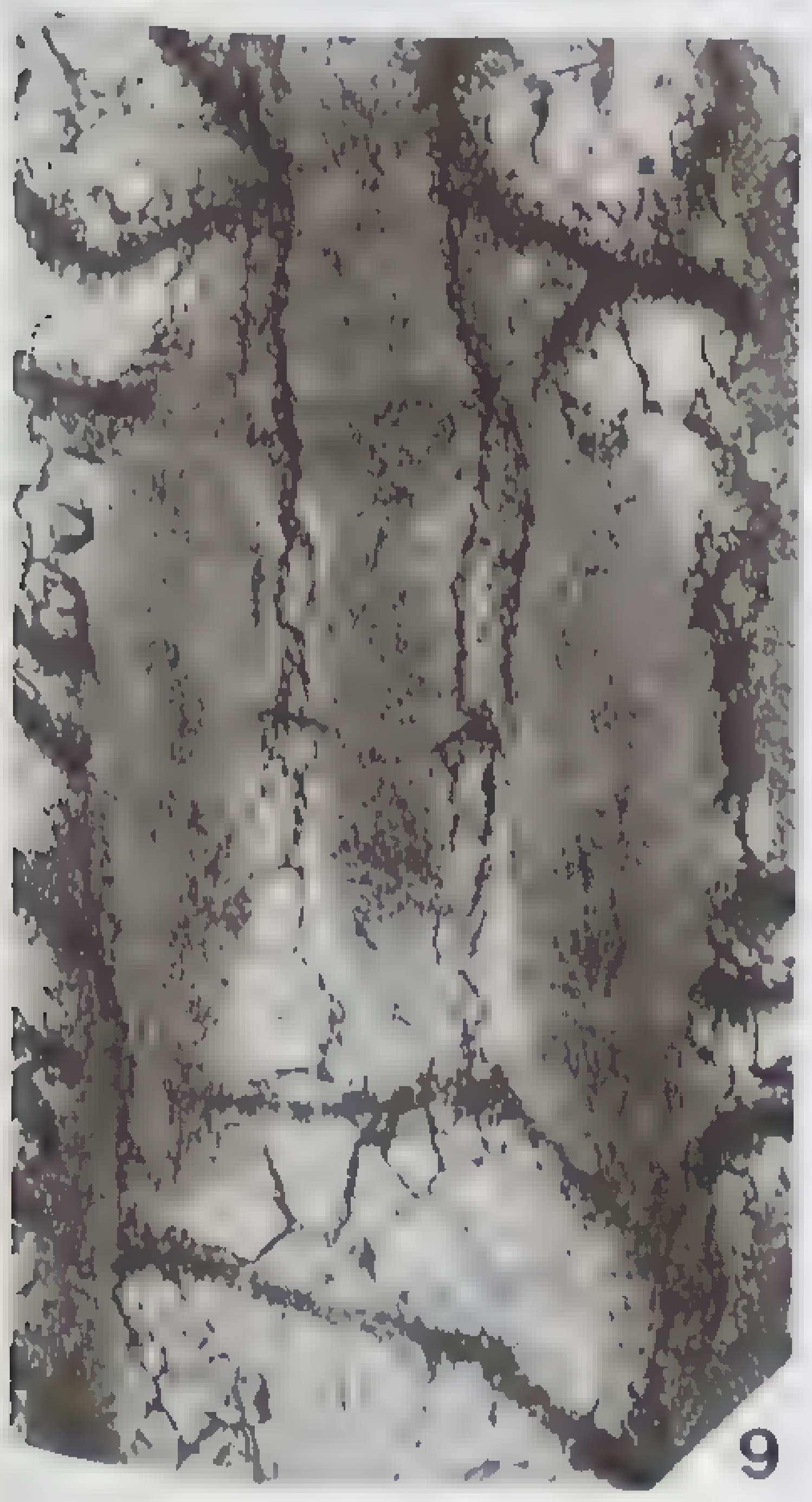
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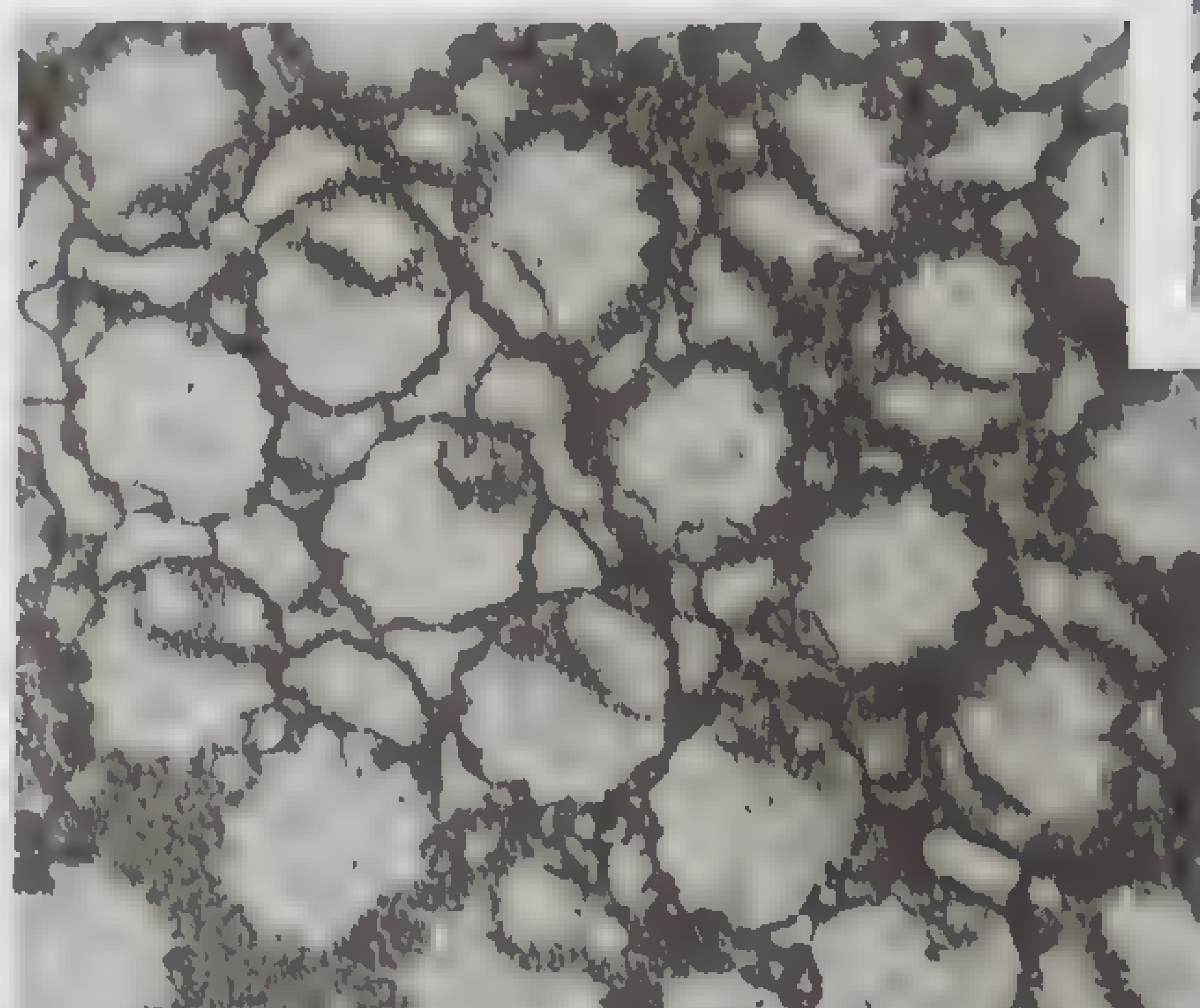
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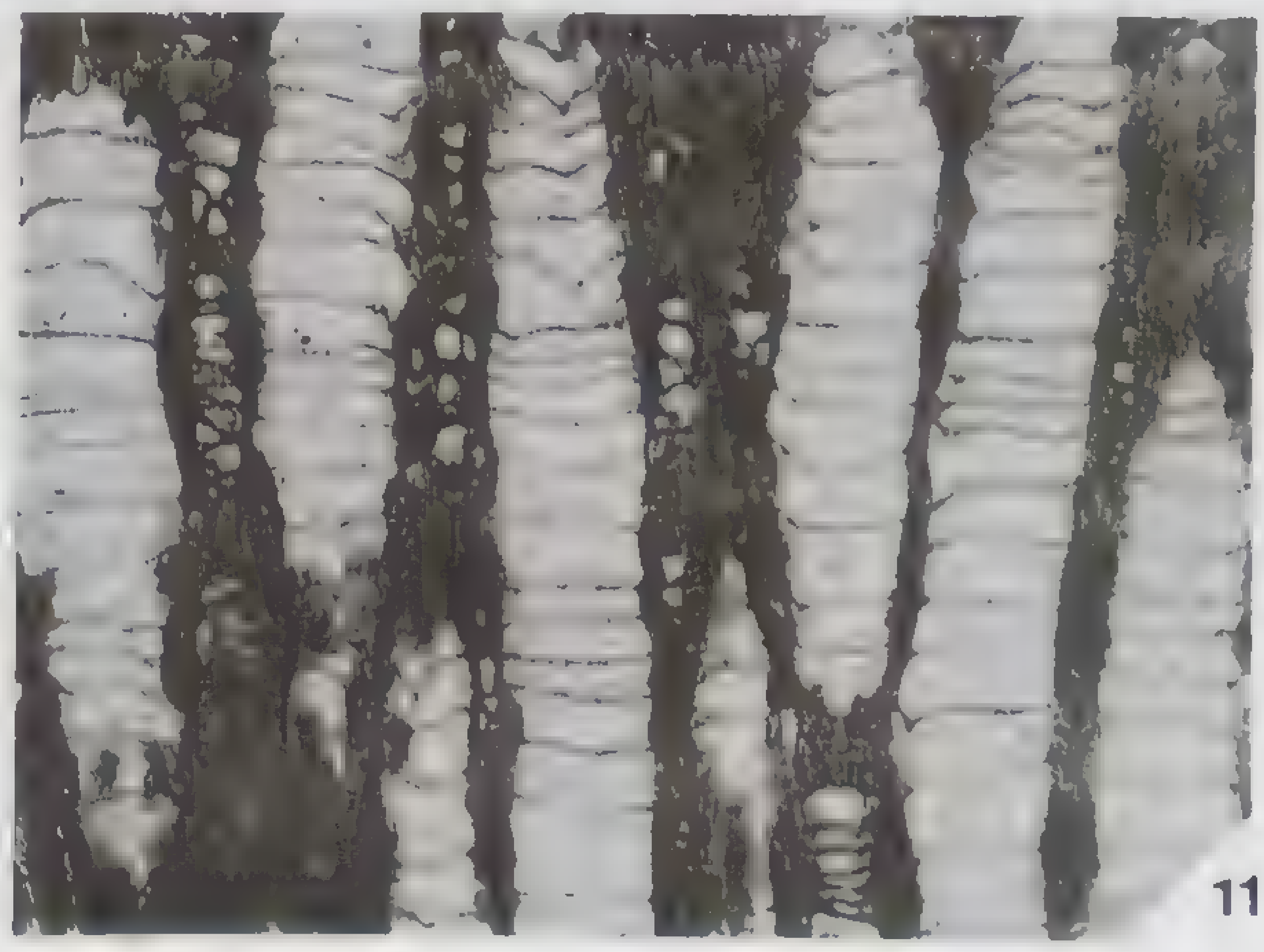
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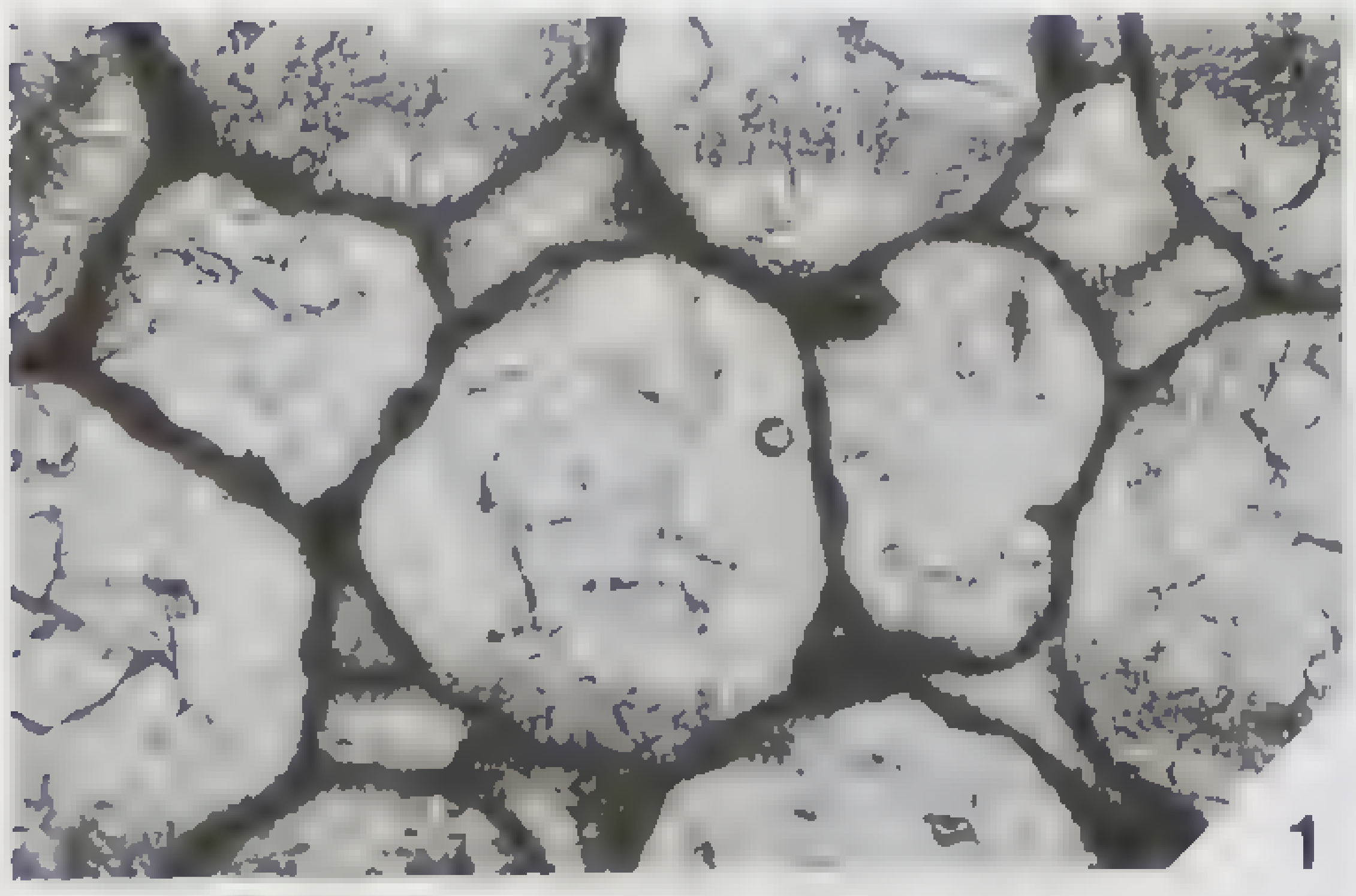
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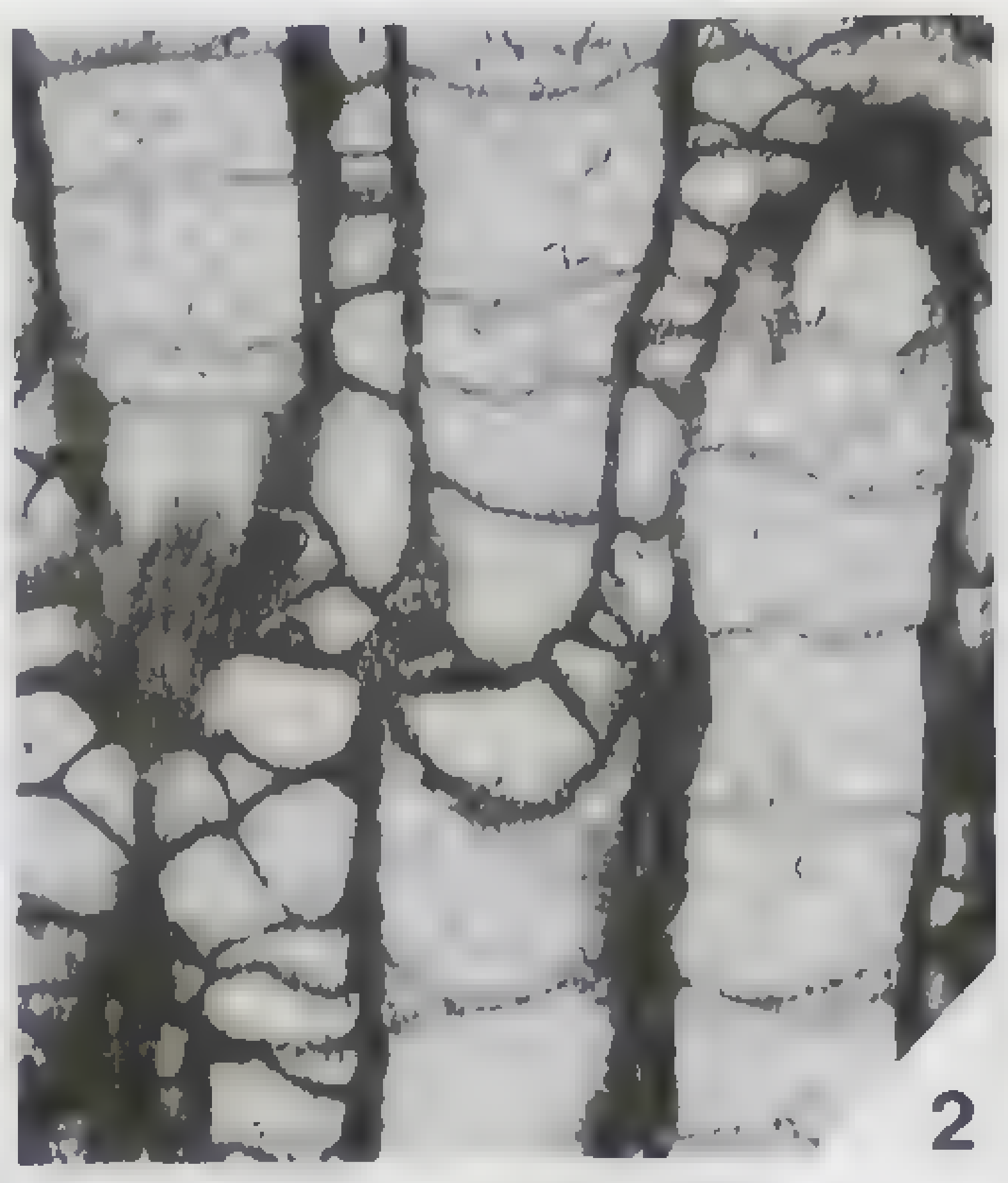
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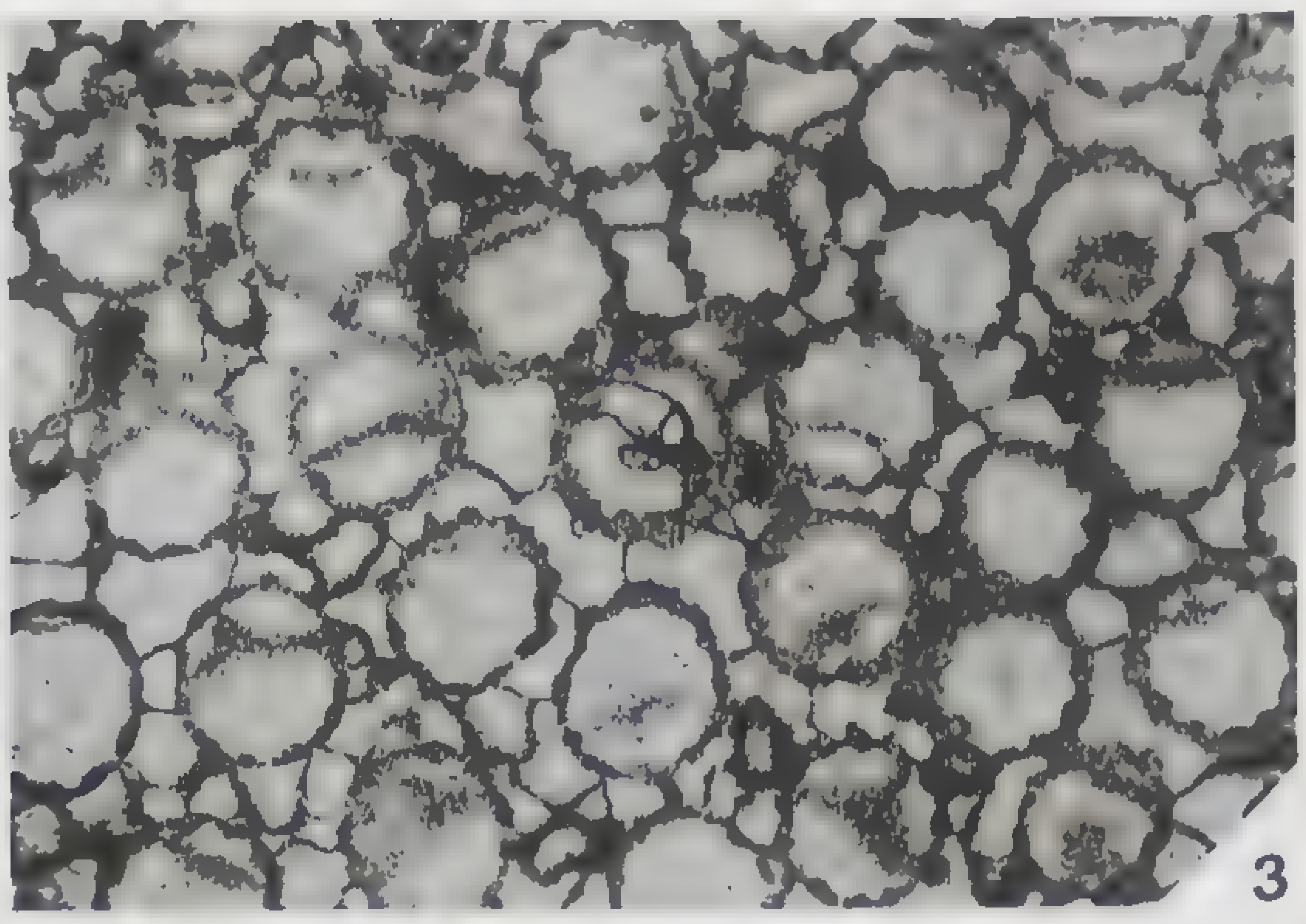
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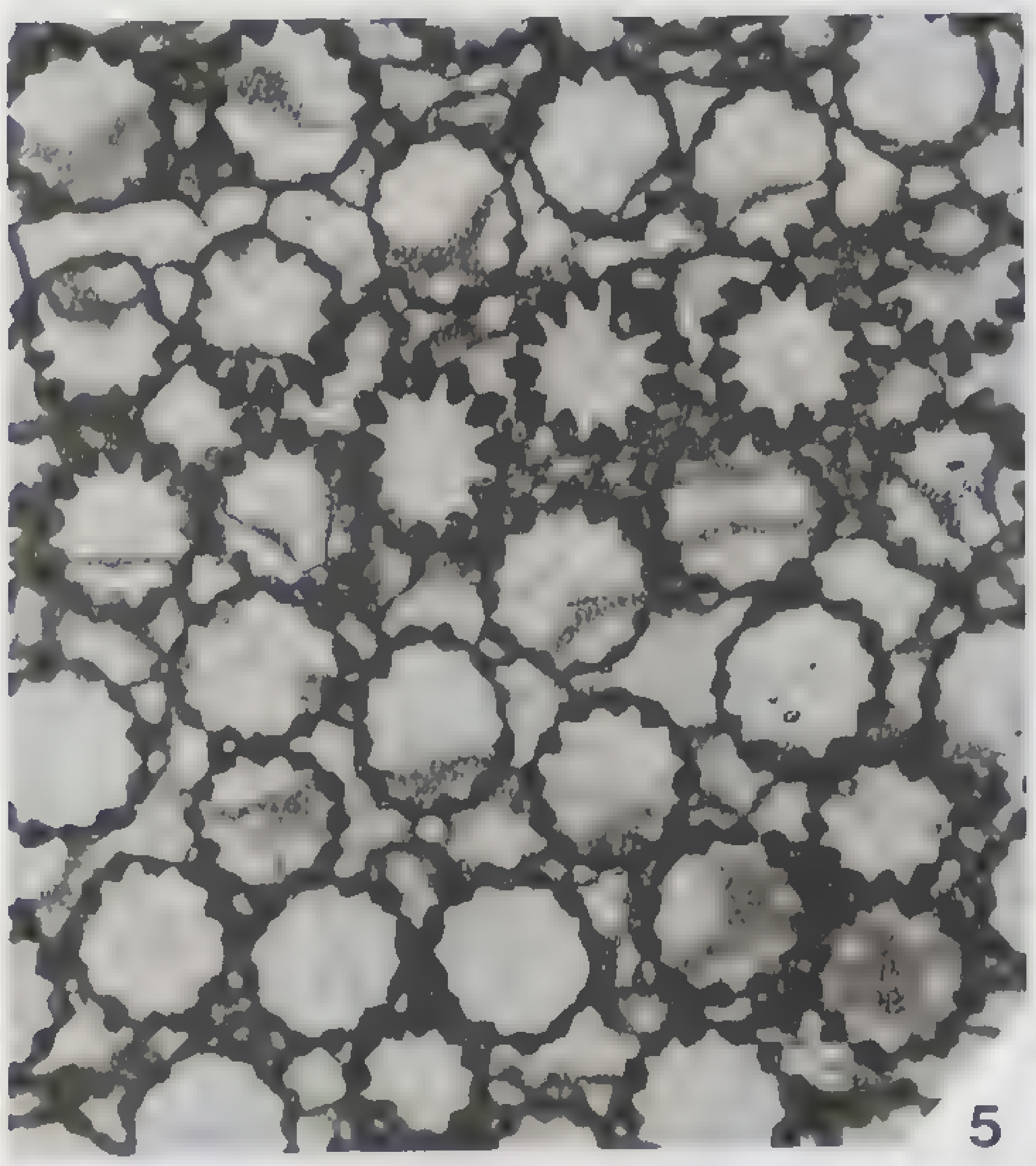
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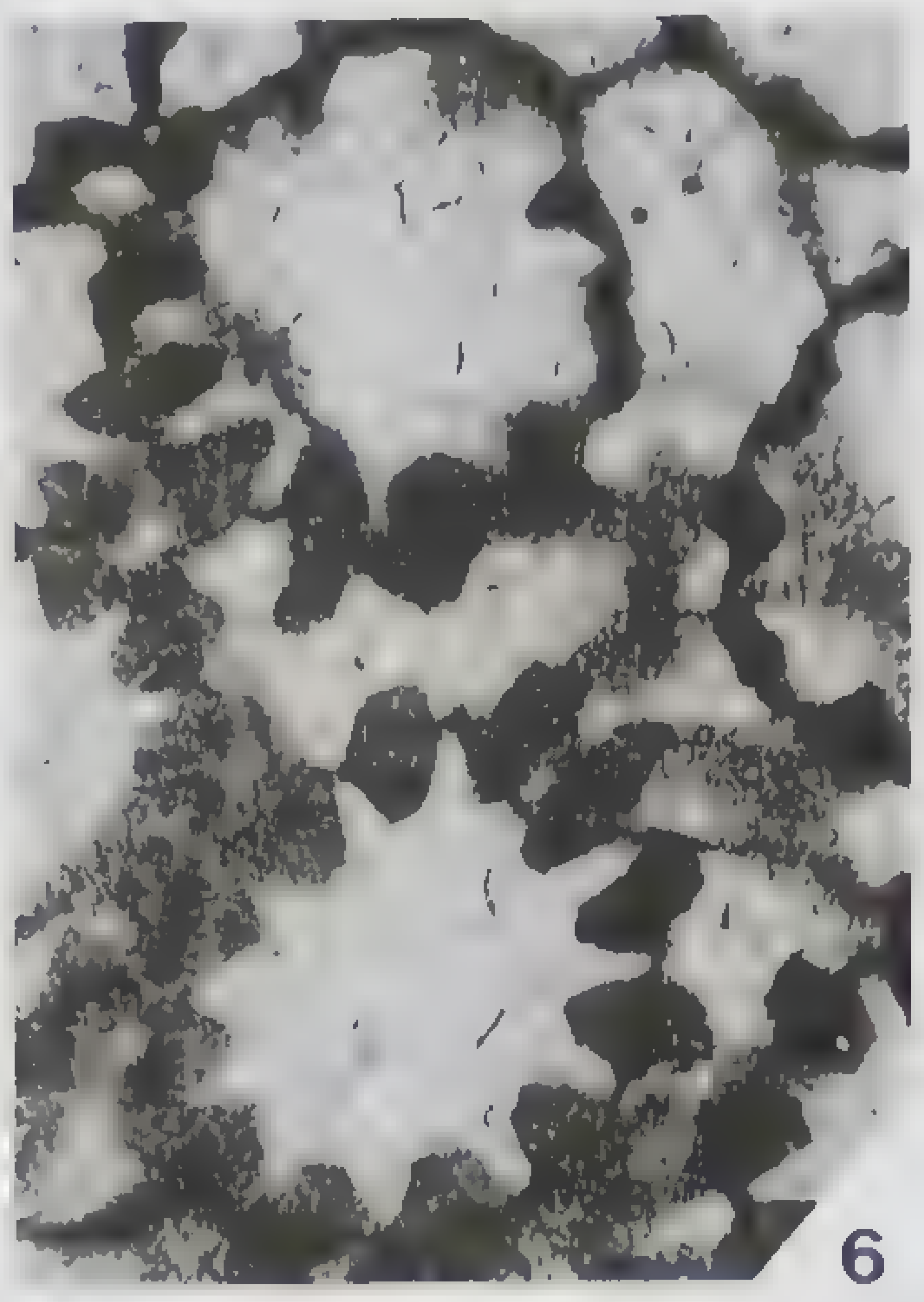
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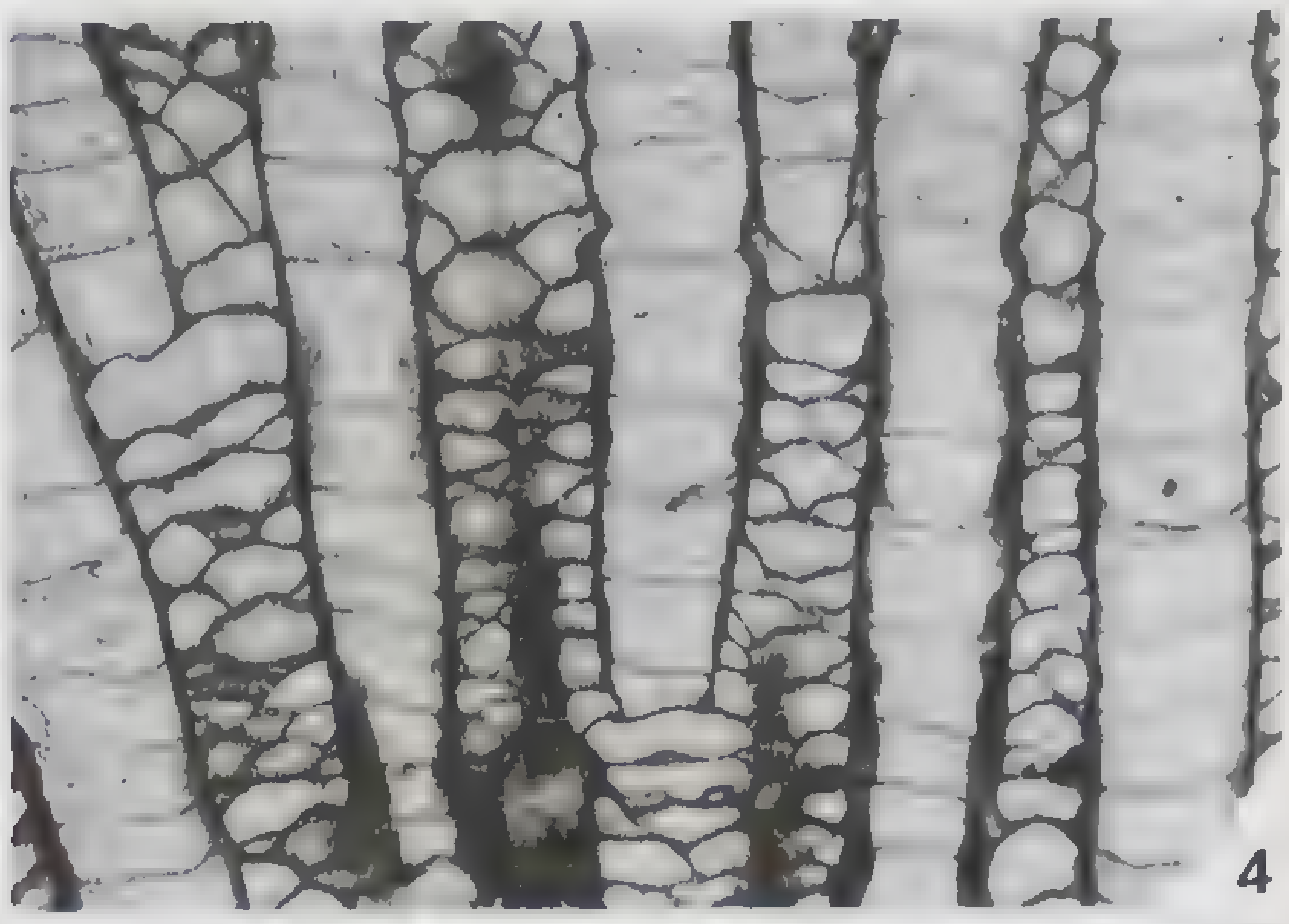
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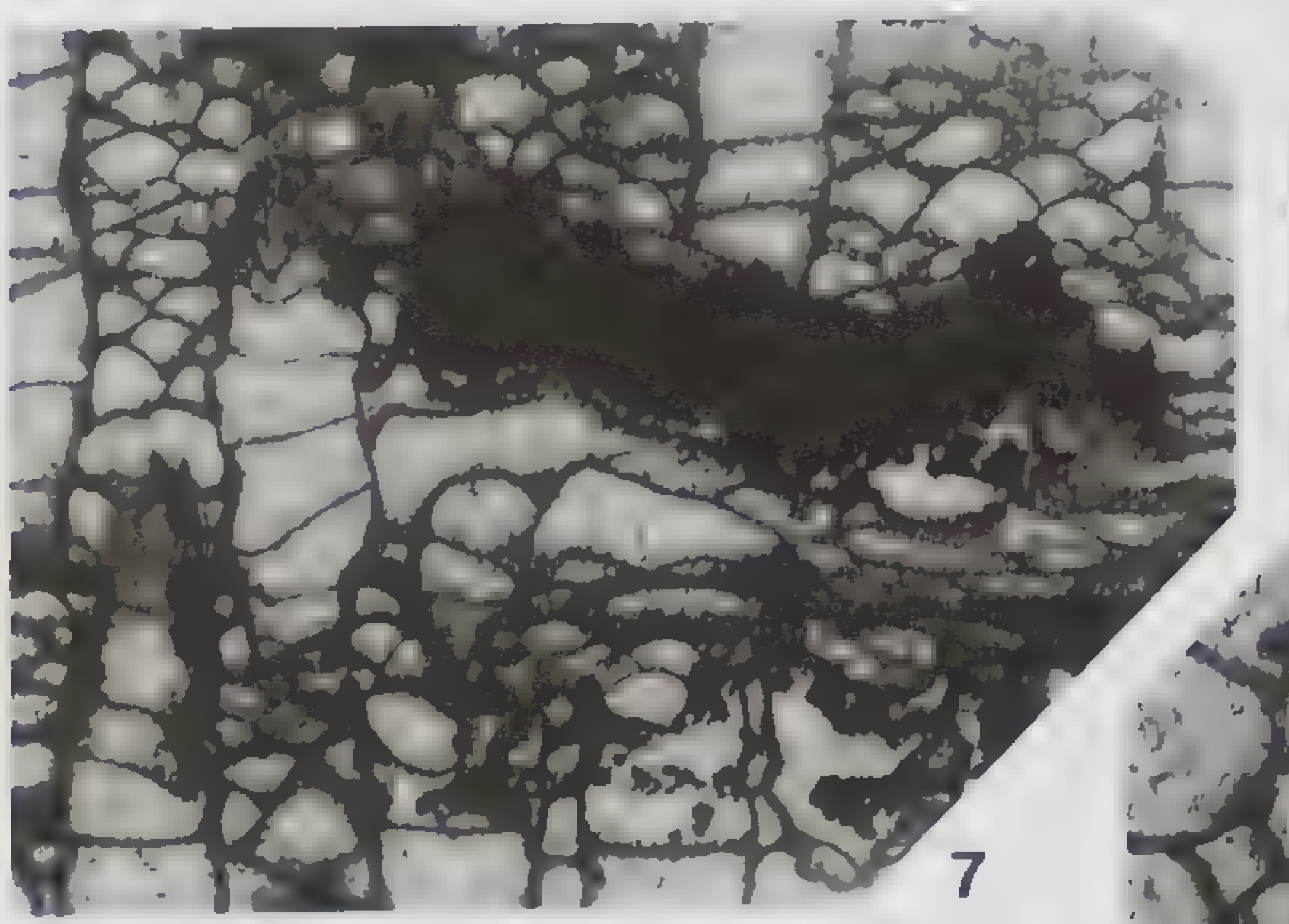
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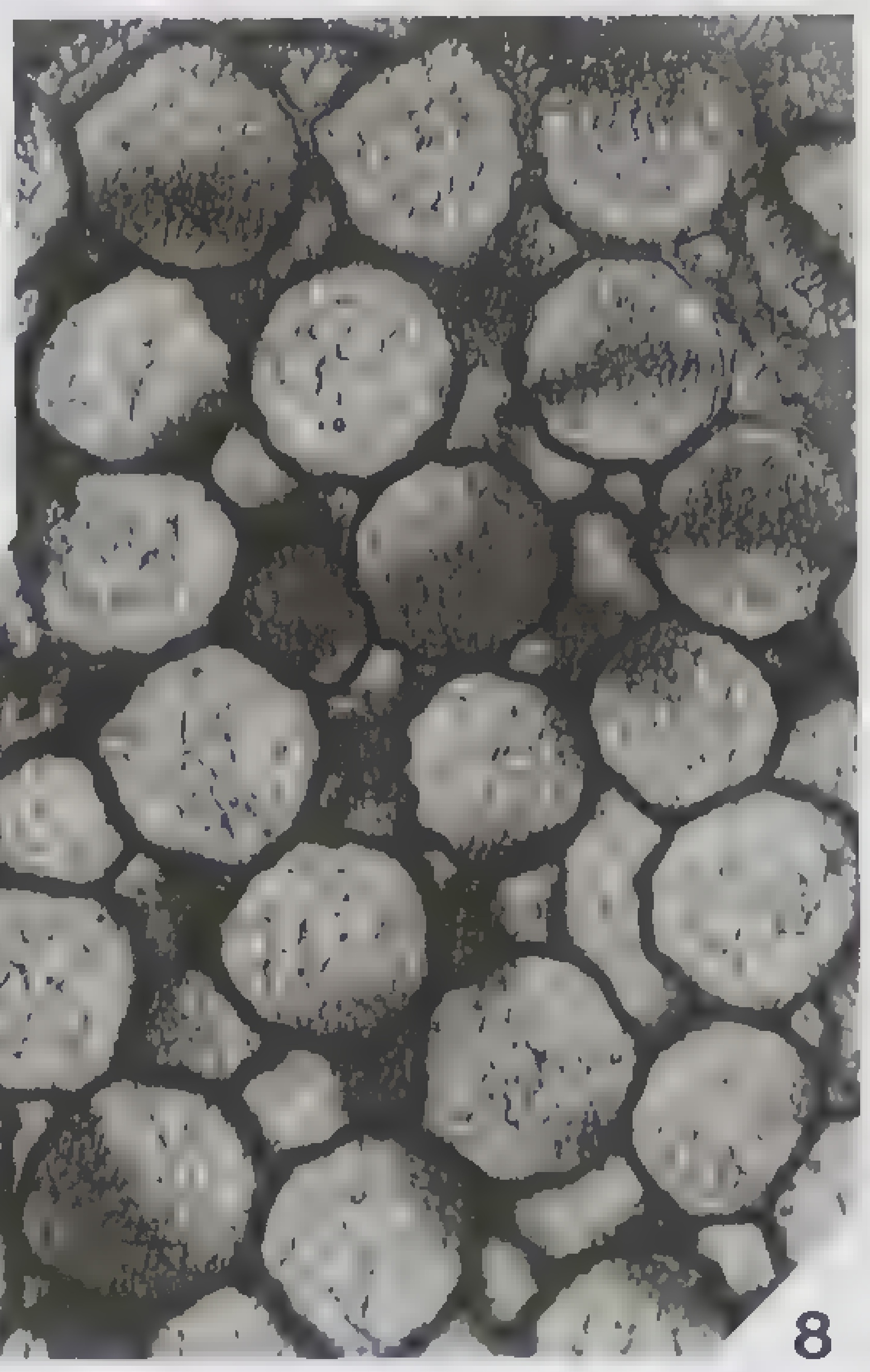
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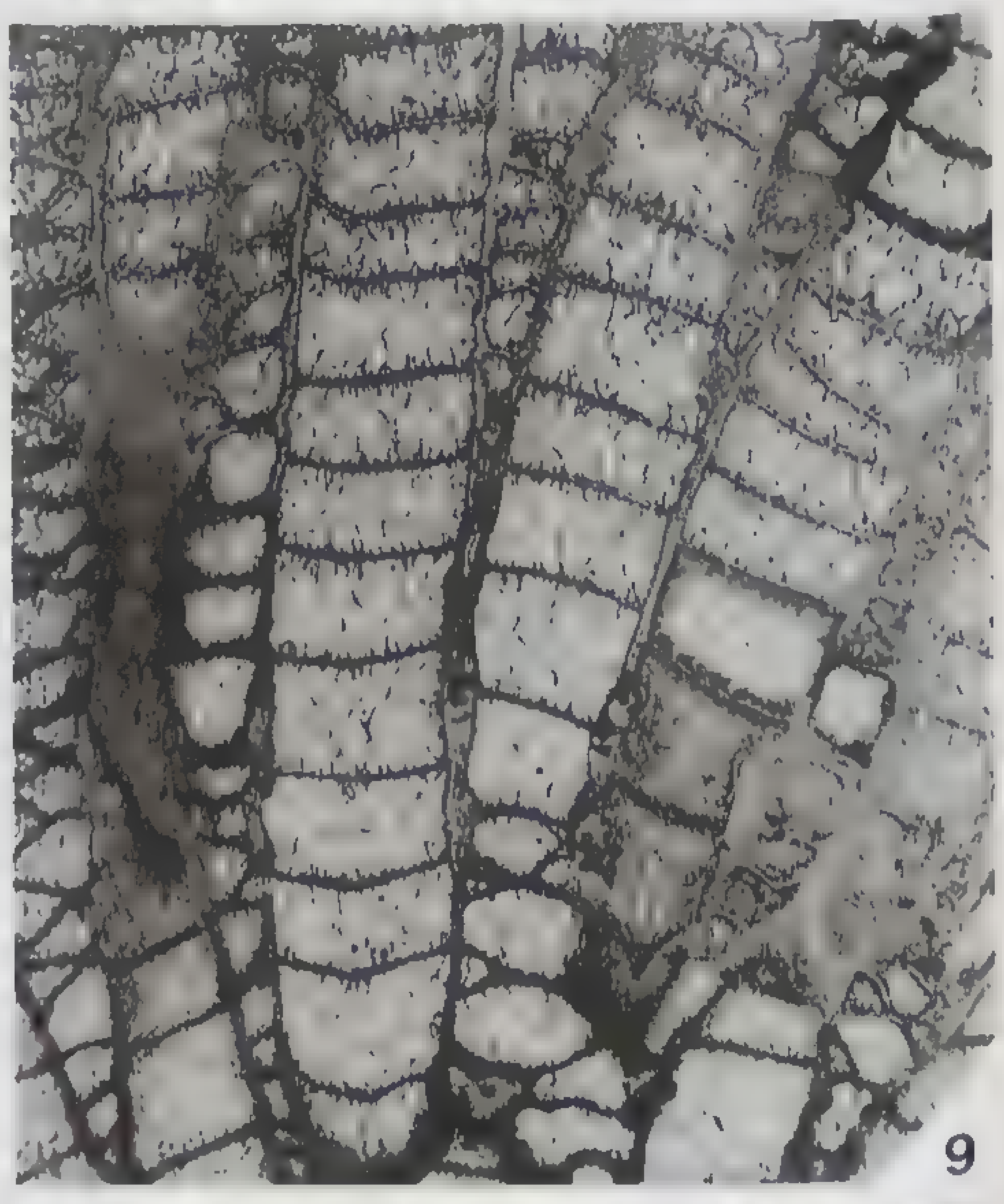
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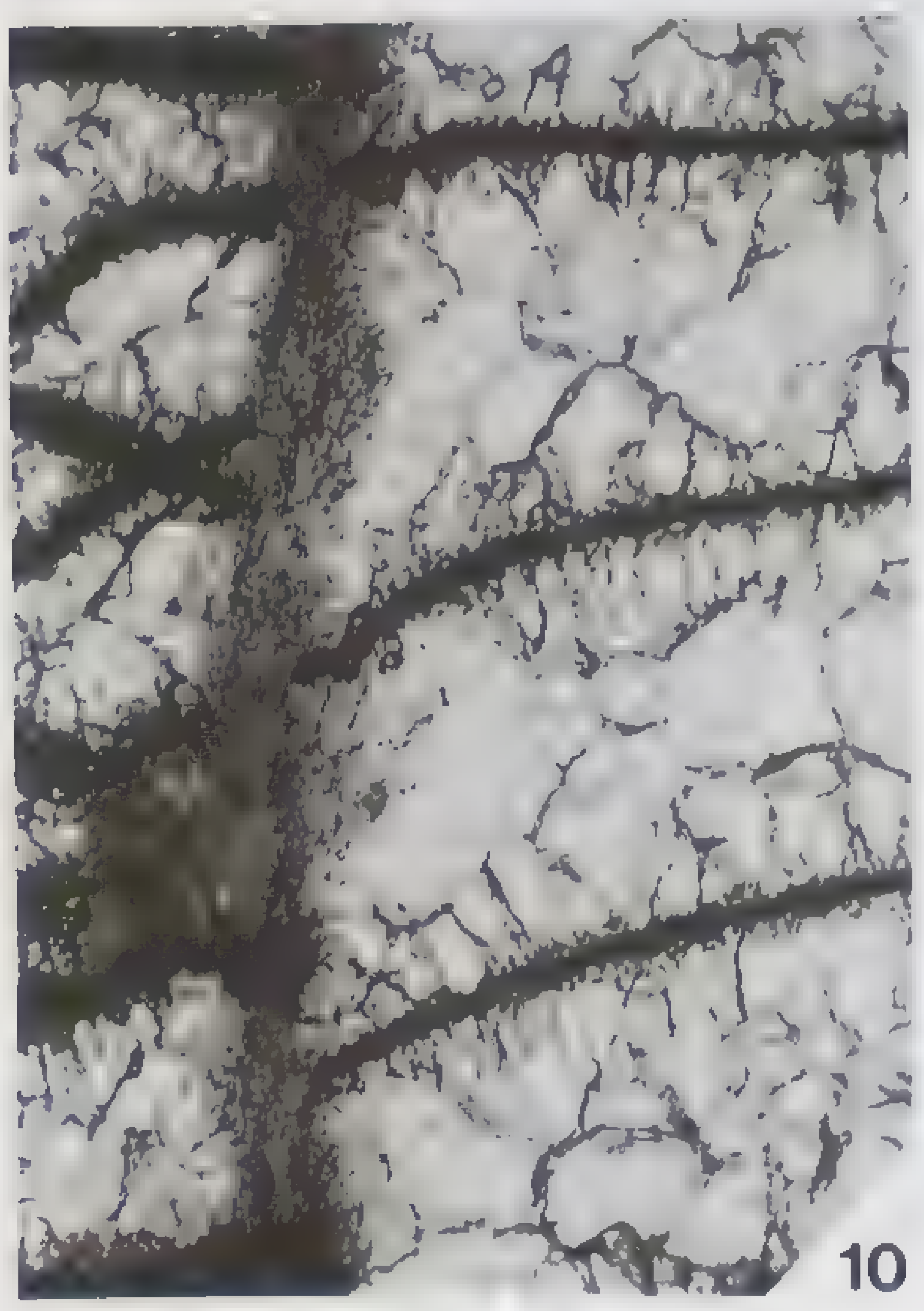
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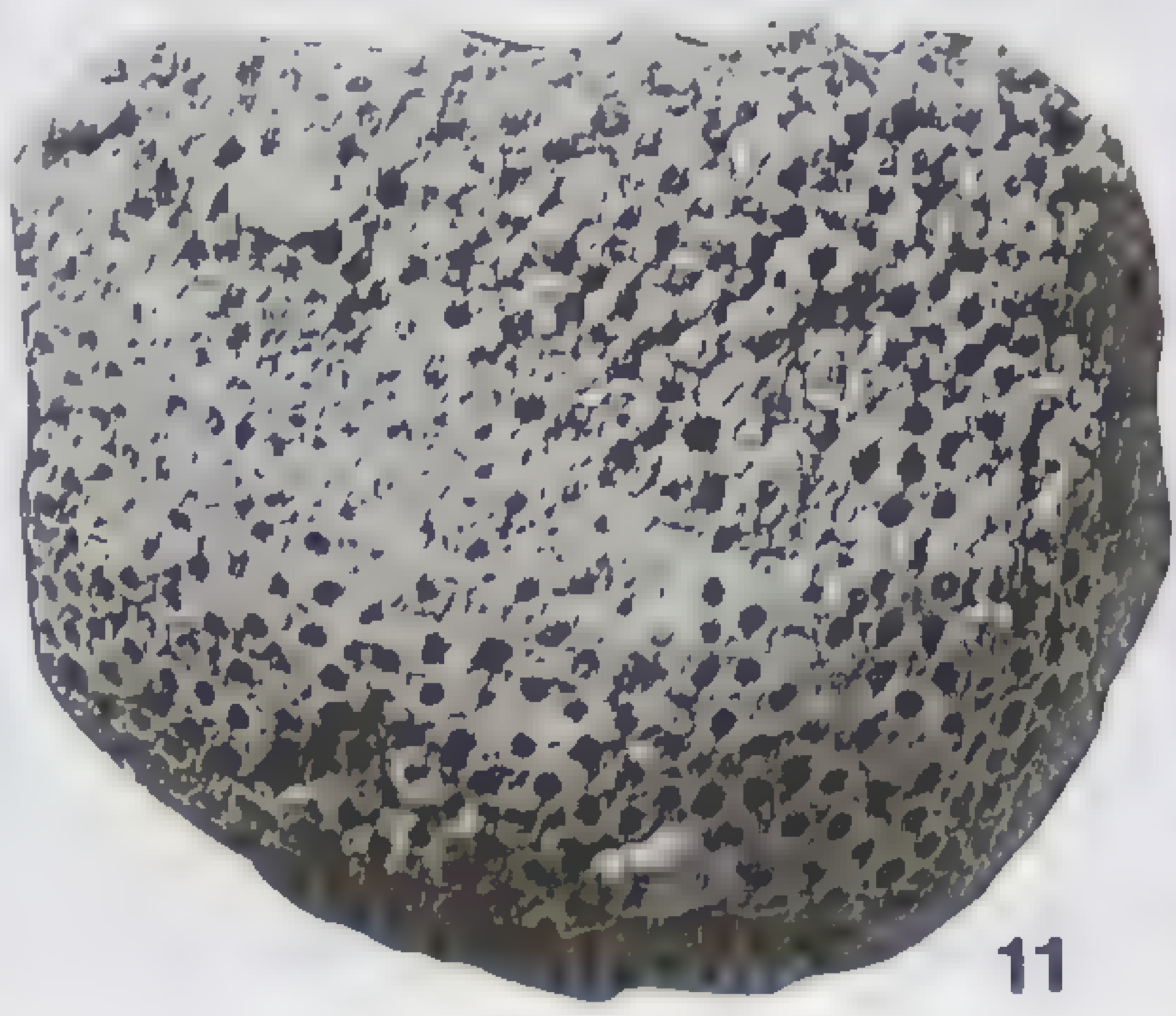
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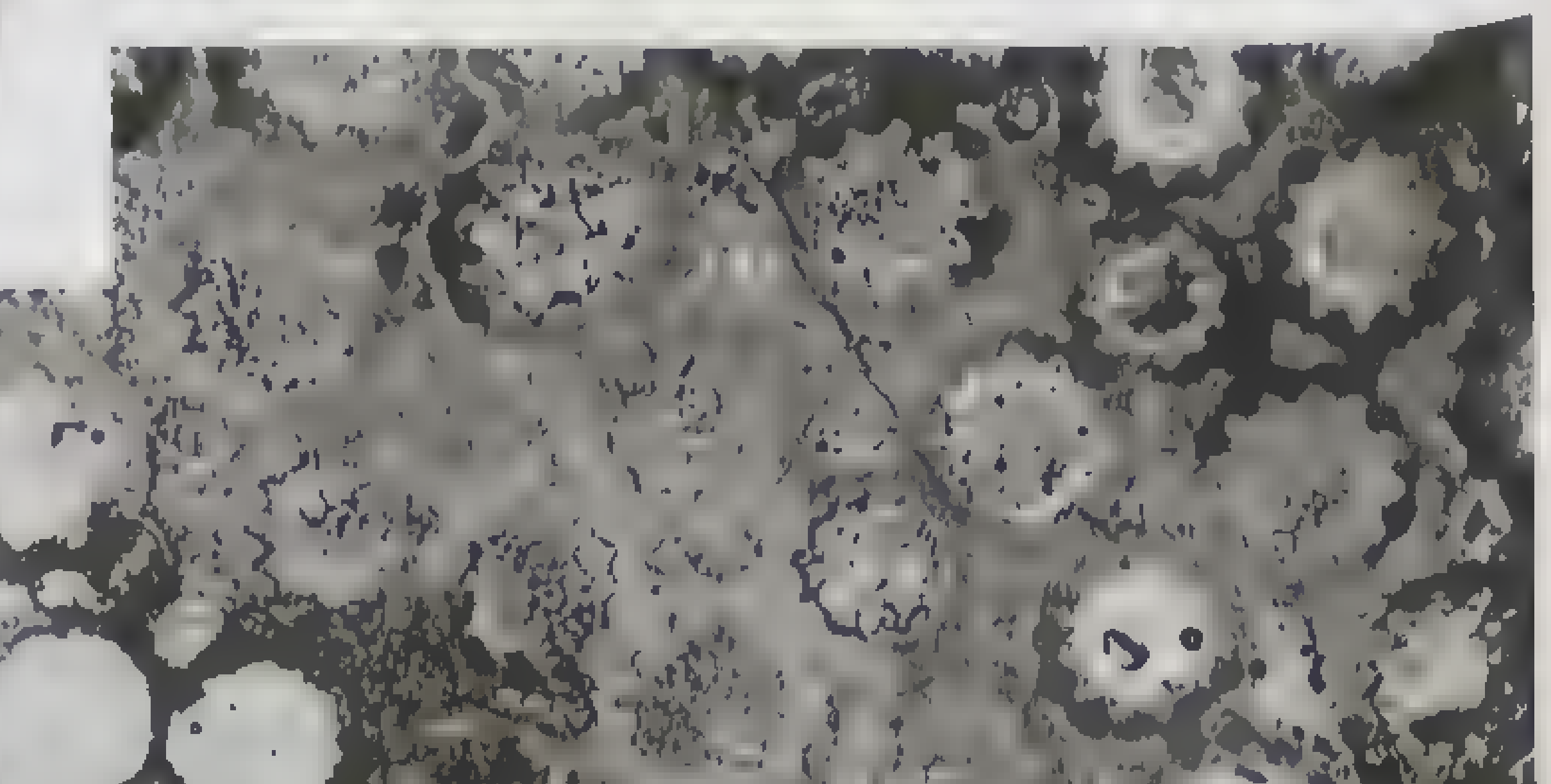
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EXPLANATION OF PLATE 2

Figure		Page
1–12.	***Propora thebesensis*** (Foerste, 1909)	45

[1–4, *Brevilamnulella* beds, Keel Formation, Section-interval 23-2 (Lawrence Quarry) (site 23iii); 5–7, oölite of Keel Formation, Section-interval 23-2a (Lawrence Quarry) (site 23i); 8–10, Leemon Formation, Section-interval 31-1 (Thebes North); 11, 12, Leemon Formation (undivided), Section 31 (Thebes North).]

1. USNM 485706b: transverse section, ×15.

2–4. USNM 459075: 2, longitudinal section showing rejuvenescence, ×12; 3, transverse section, ×8; 4, longitudinal section, ×8.

5, 6. USNM 485709: 5, transverse section, ×8; 6, transverse section (detail from upper left of center in 5, turned 50° clockwise), ×20.

7. USNM 485708: longitudinal section showing sediment inclusion and regeneration, ×12.

8–10. USNM 485711: 8, transverse section, ×8; 9, longitudinal section, ×8; 10, longitudinal section showing tabularium wall, ×40.

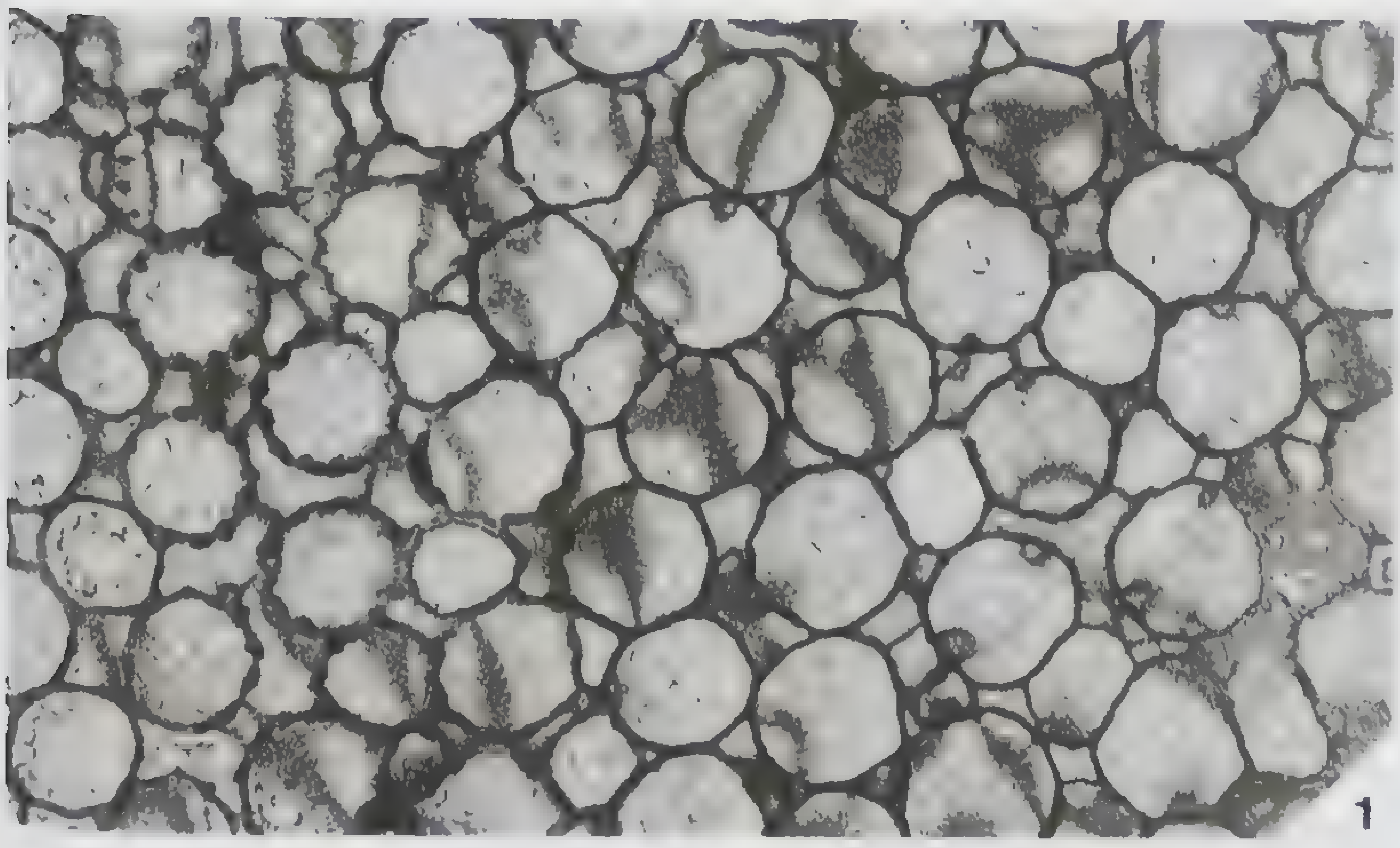
11, 12. UI X-908: 11, exterior lateral view of corallum, ×1.5; 12, transverse section, ×8.

EXPLANATION OF PLATE 3

Figure		Page
1–11.	***Propora thebesensis*** (Foerste, 1909)	45

[1–3, Leemon Formation (undivided), Section 31 (Thebes North); 4, Leemon Formation, Section-interval 31-1 (Thebes North); 5, Bryant Knob Formation (undivided), 5 km south of Clarksville, Missouri; 6, 7, Kissenger Limestone Member, Bryant Knob Formation, Section-interval 18-4 (Kissenger); 8–11, Kissenger Limestone Member, Bryant Knob Formation, Section-interval 16-2 (Clinton Spring).]

1, 2. USNM 84863b (lectotype): 1, transverse section, ×8; 2, exterior lateral view of corallum, ×1.5.
3. USNM 84863a (paralectotype): exterior basal view of corallum, ×2.
4. USNM 485715: longitudinal section through entire corallum (note abraded base), ×2.
5. UI C-1466b: transverse section, ×8.
6, 7. USNM 459084: 6, transverse section, ×8; 7, longitudinal section, ×8.
8–11. USNM 459076: 8, longitudinal section through entire corallum (note abrasion at base), ×2; 9, transverse section, ×8; 10, longitudinal section (detail from lower left of center in 8, turned 20° counterclockwise), ×8; 11, longitudinal section through base of a tabularium (detail from center of 10), ×15.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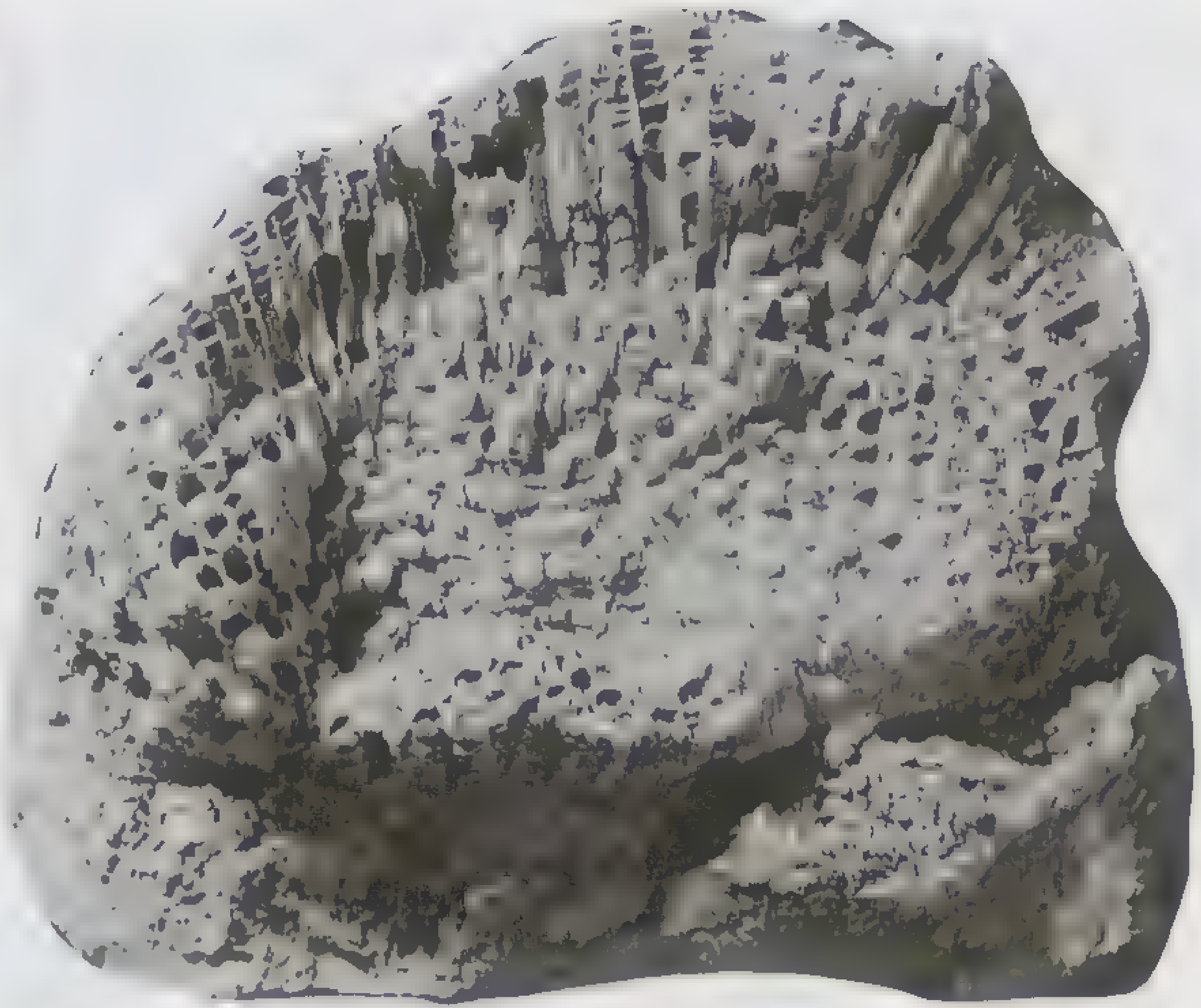
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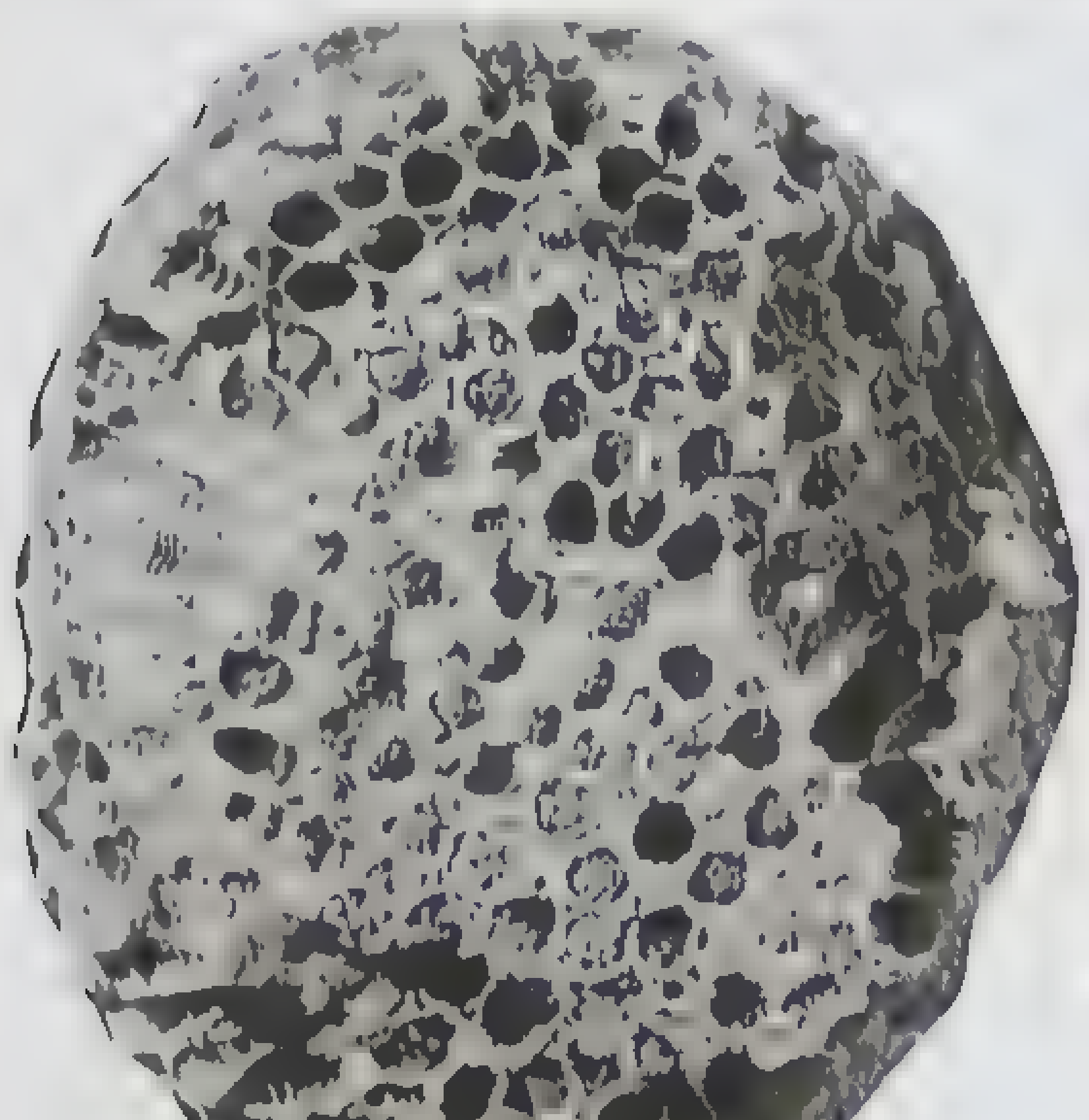
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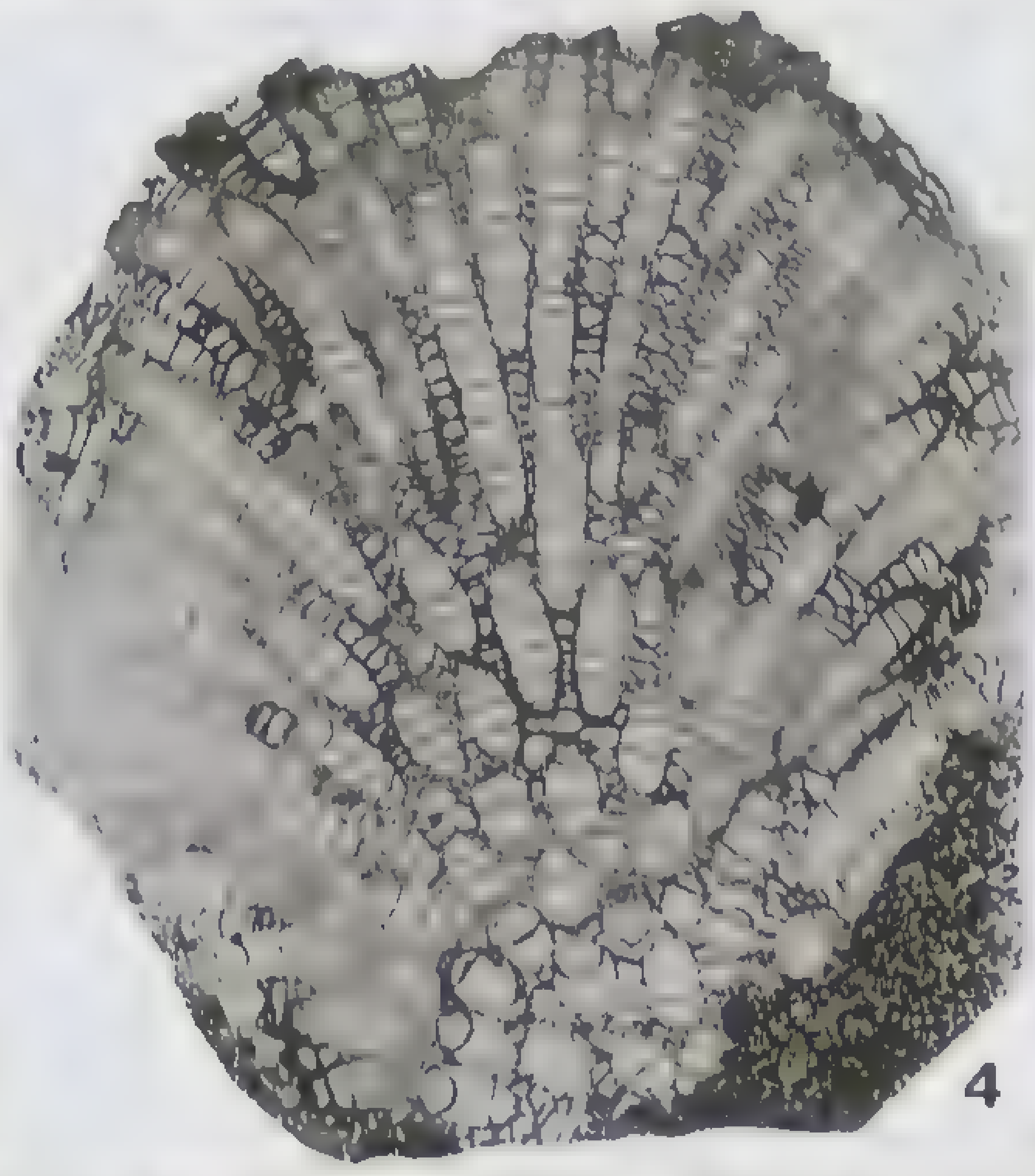
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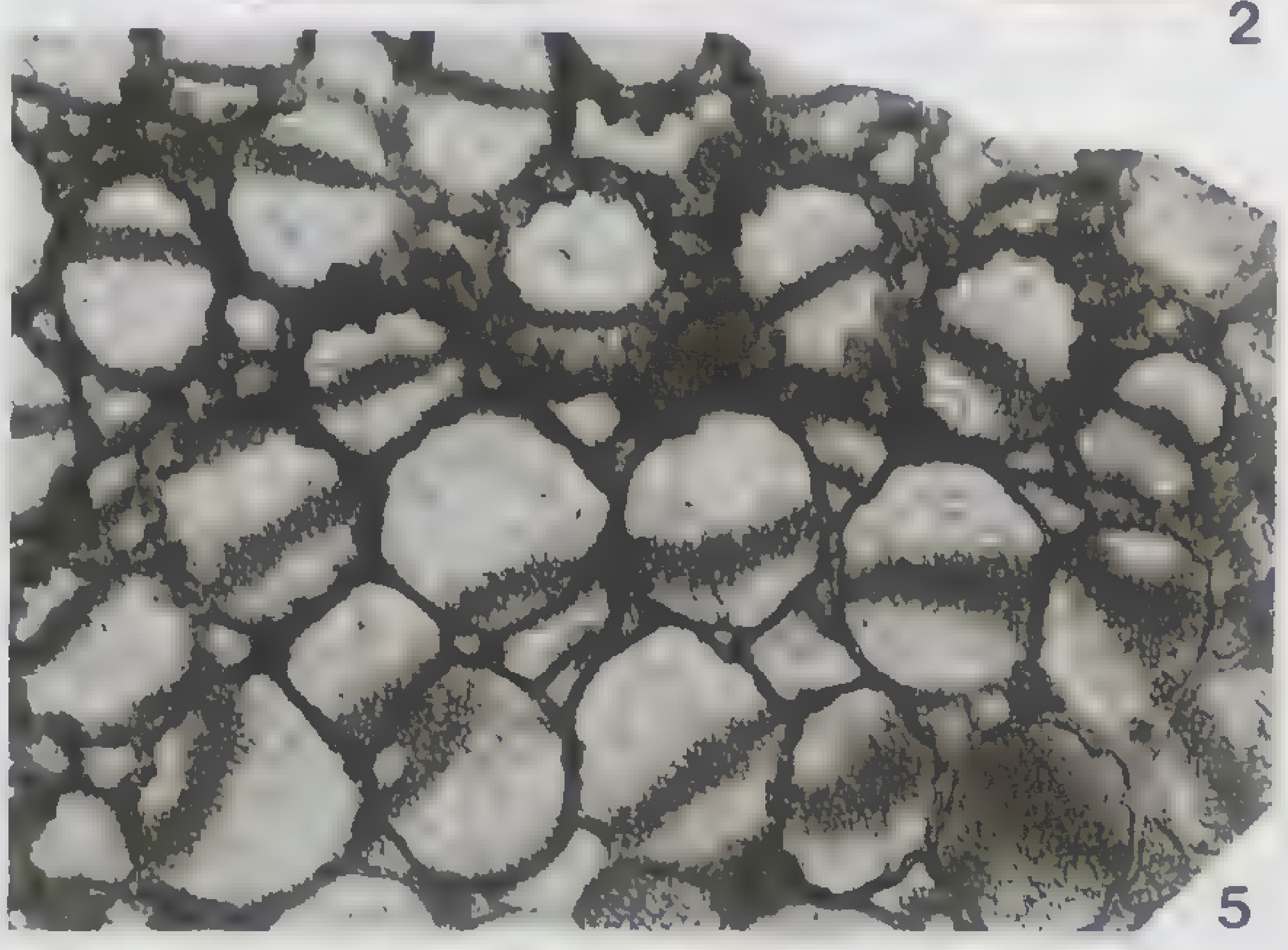
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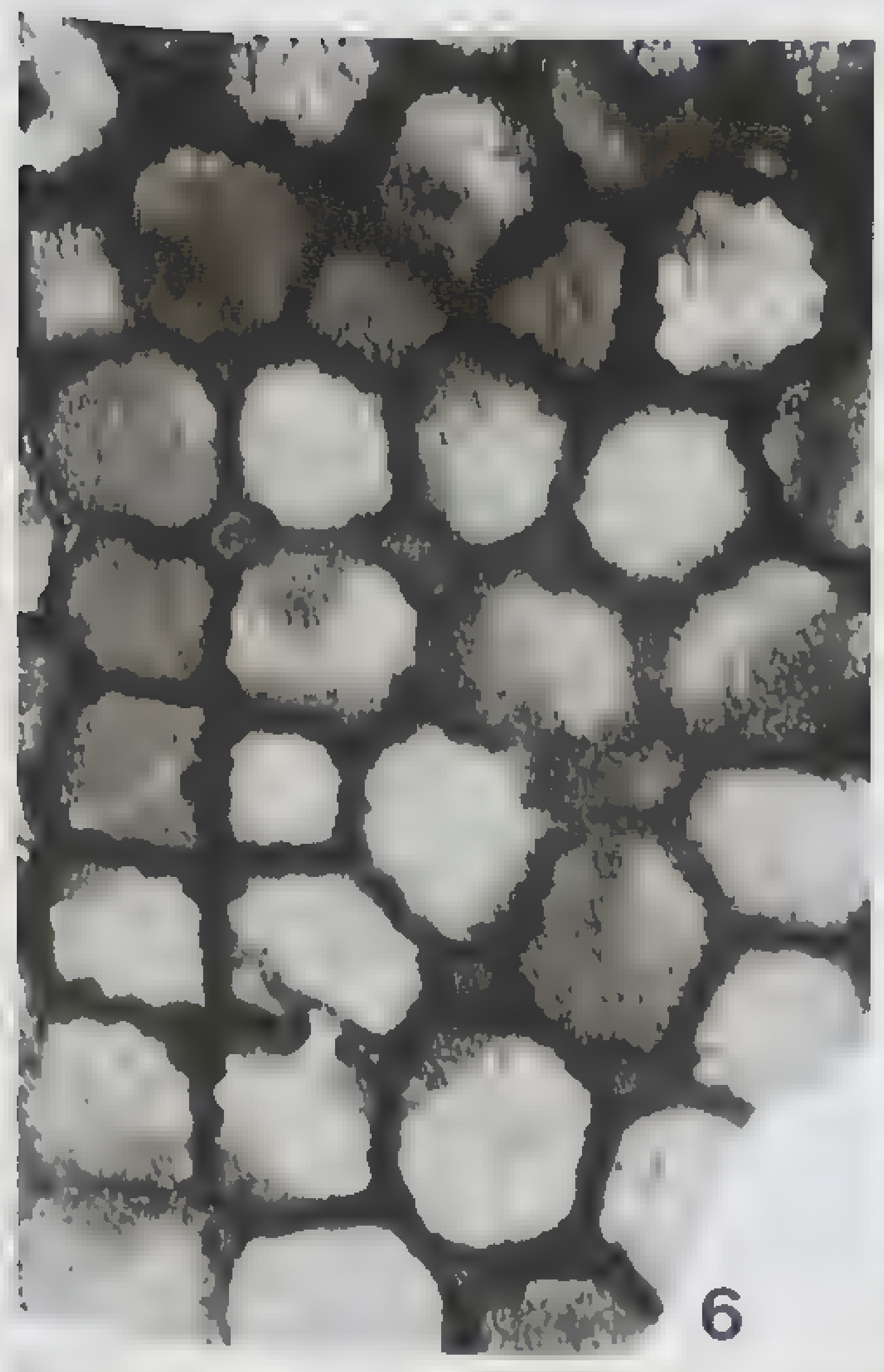
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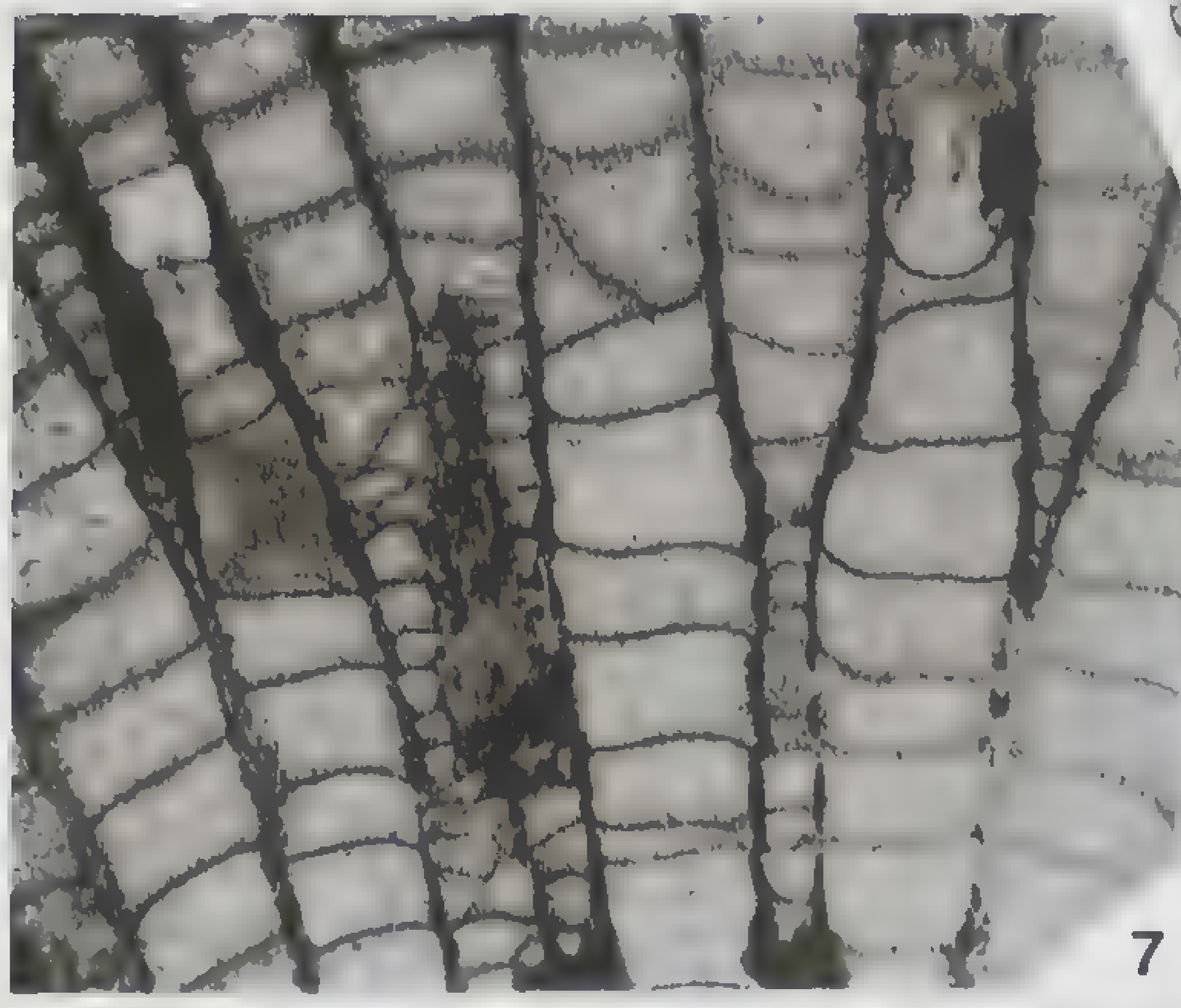
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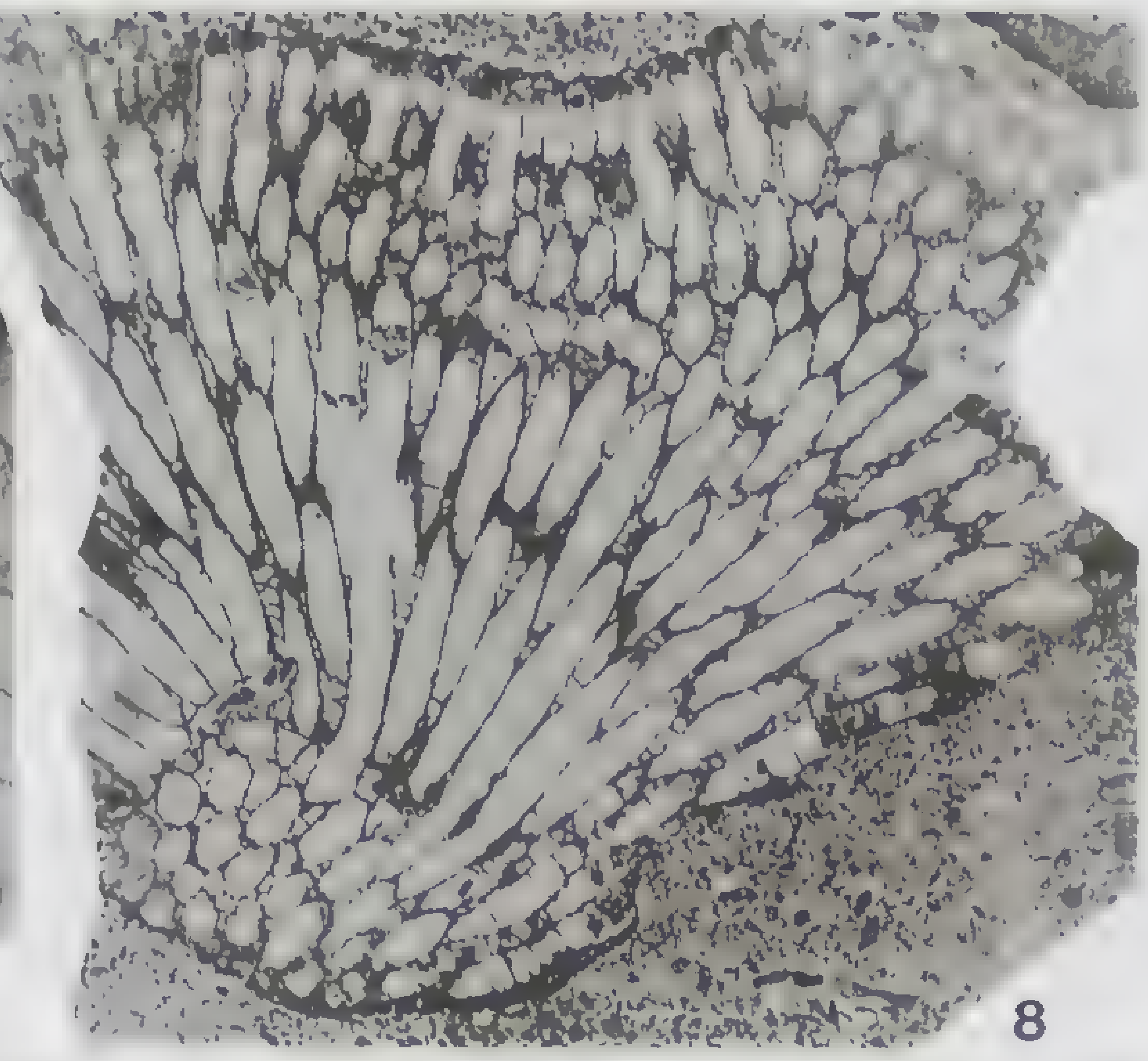
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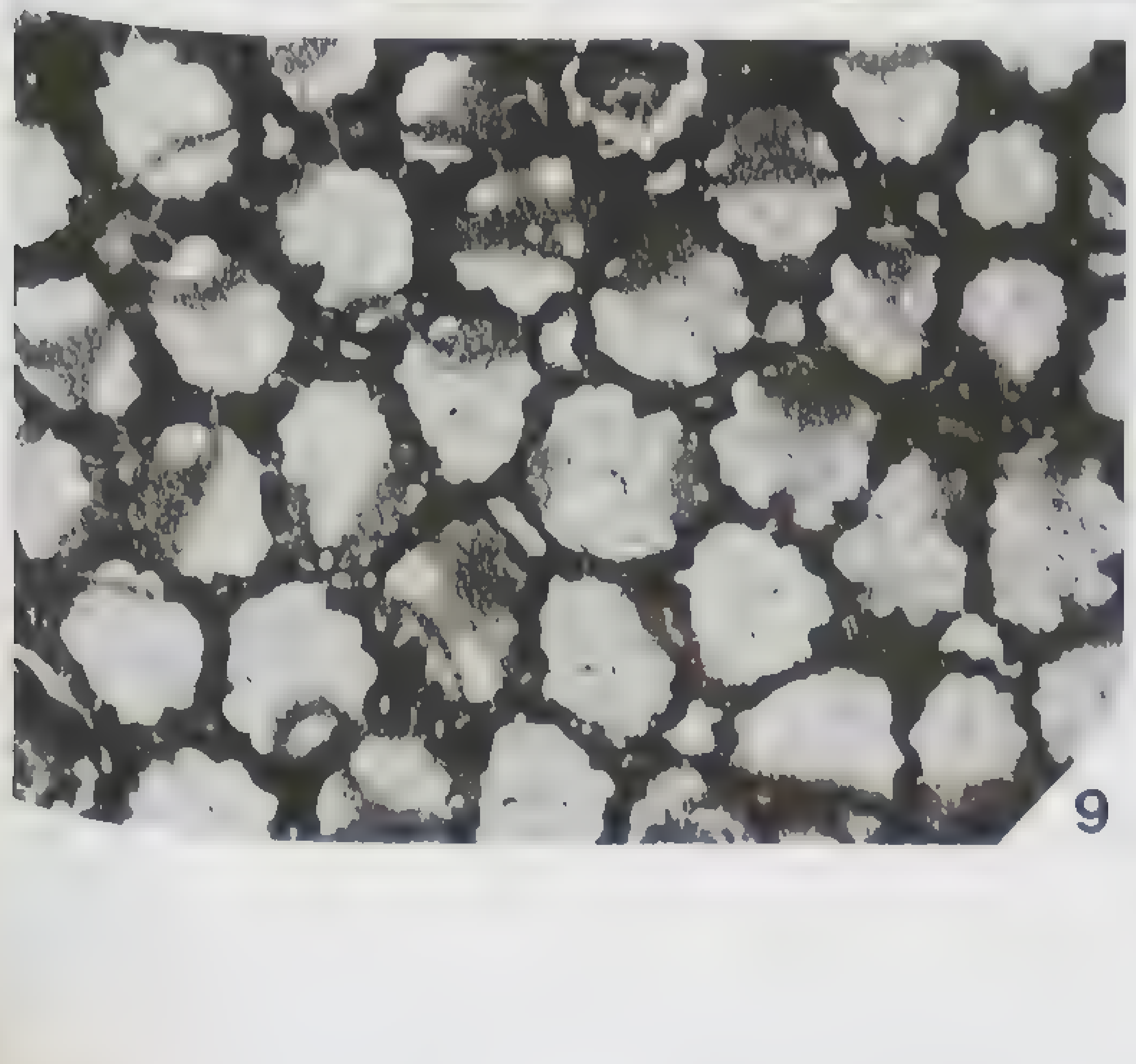
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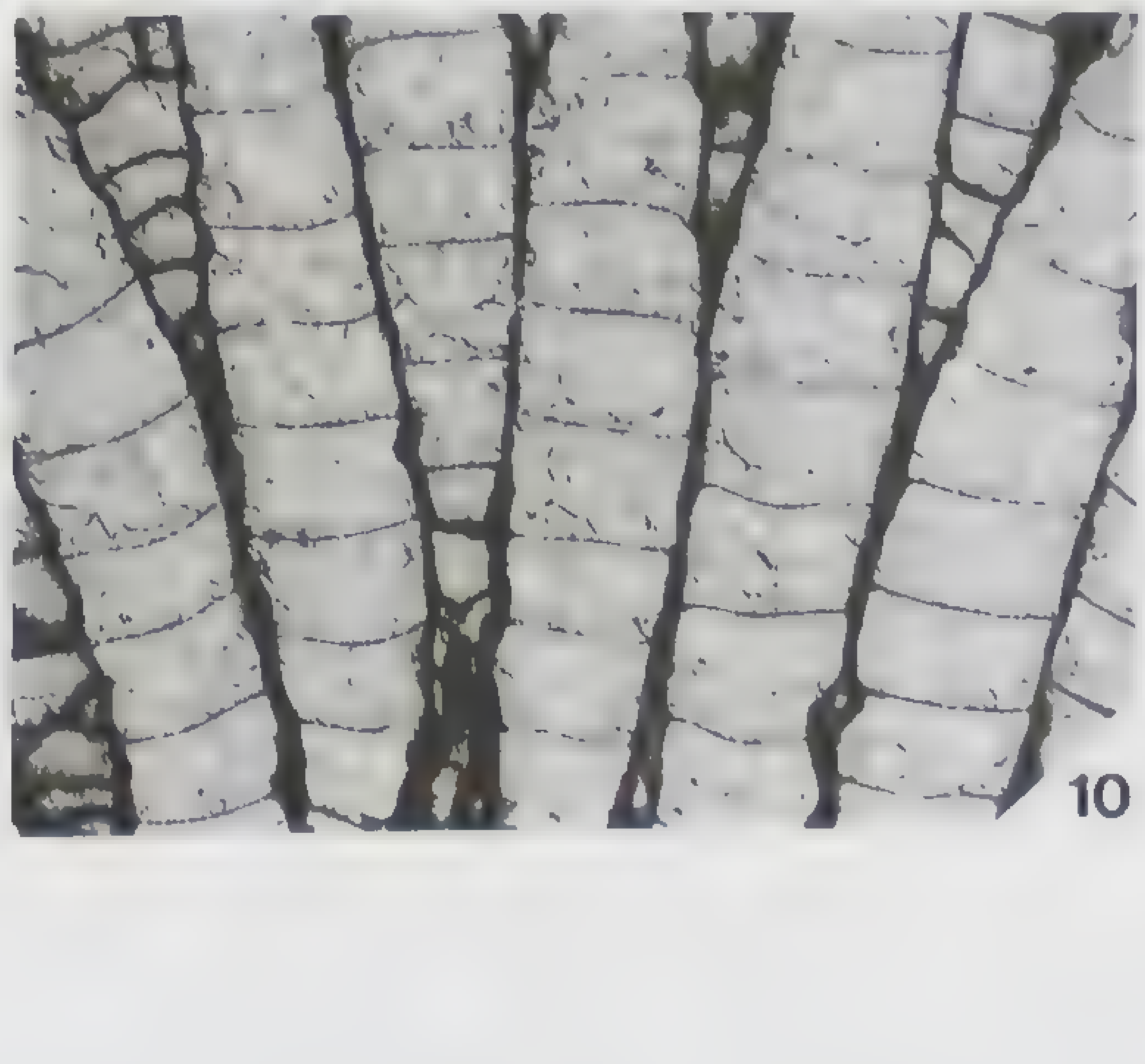
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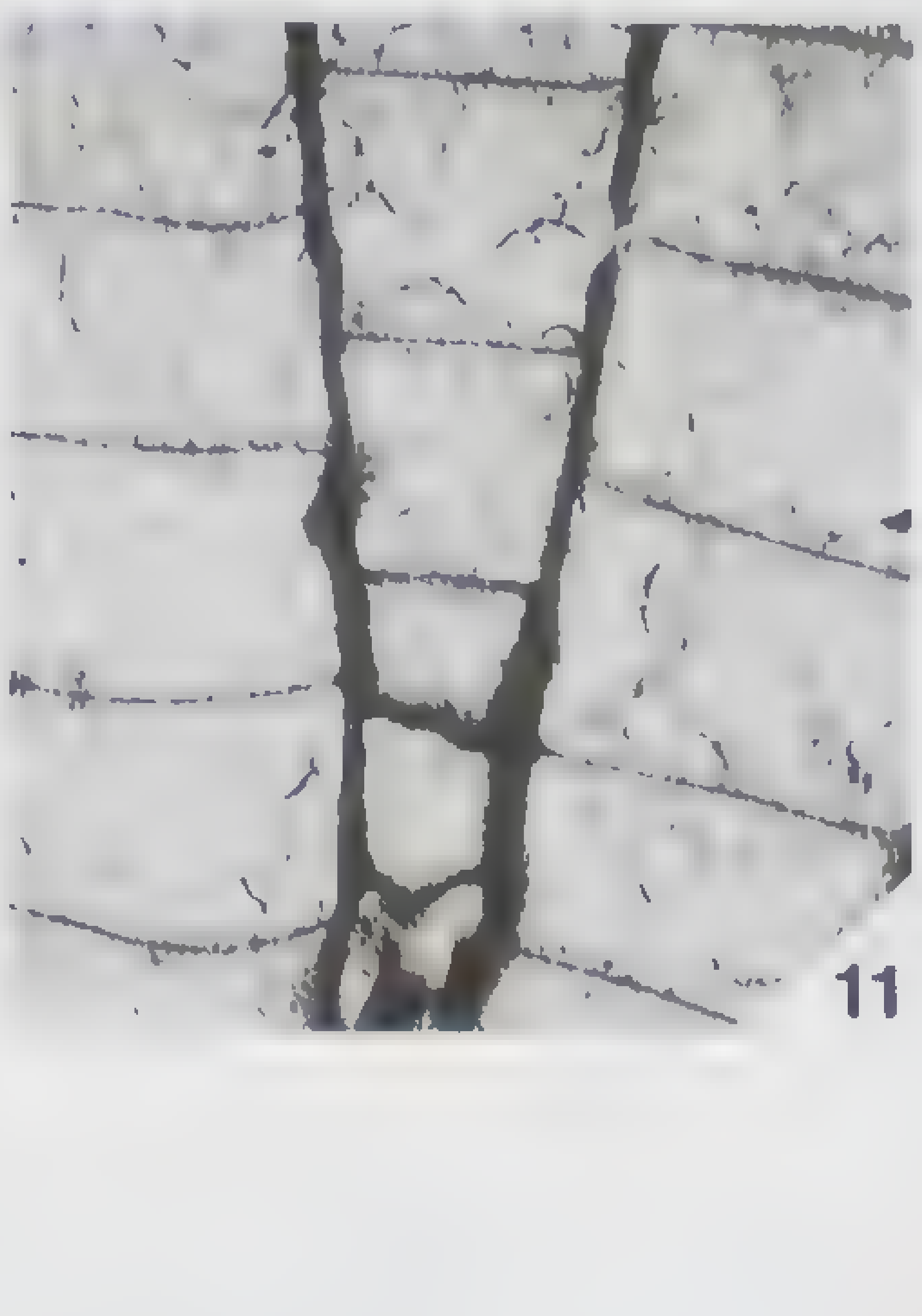
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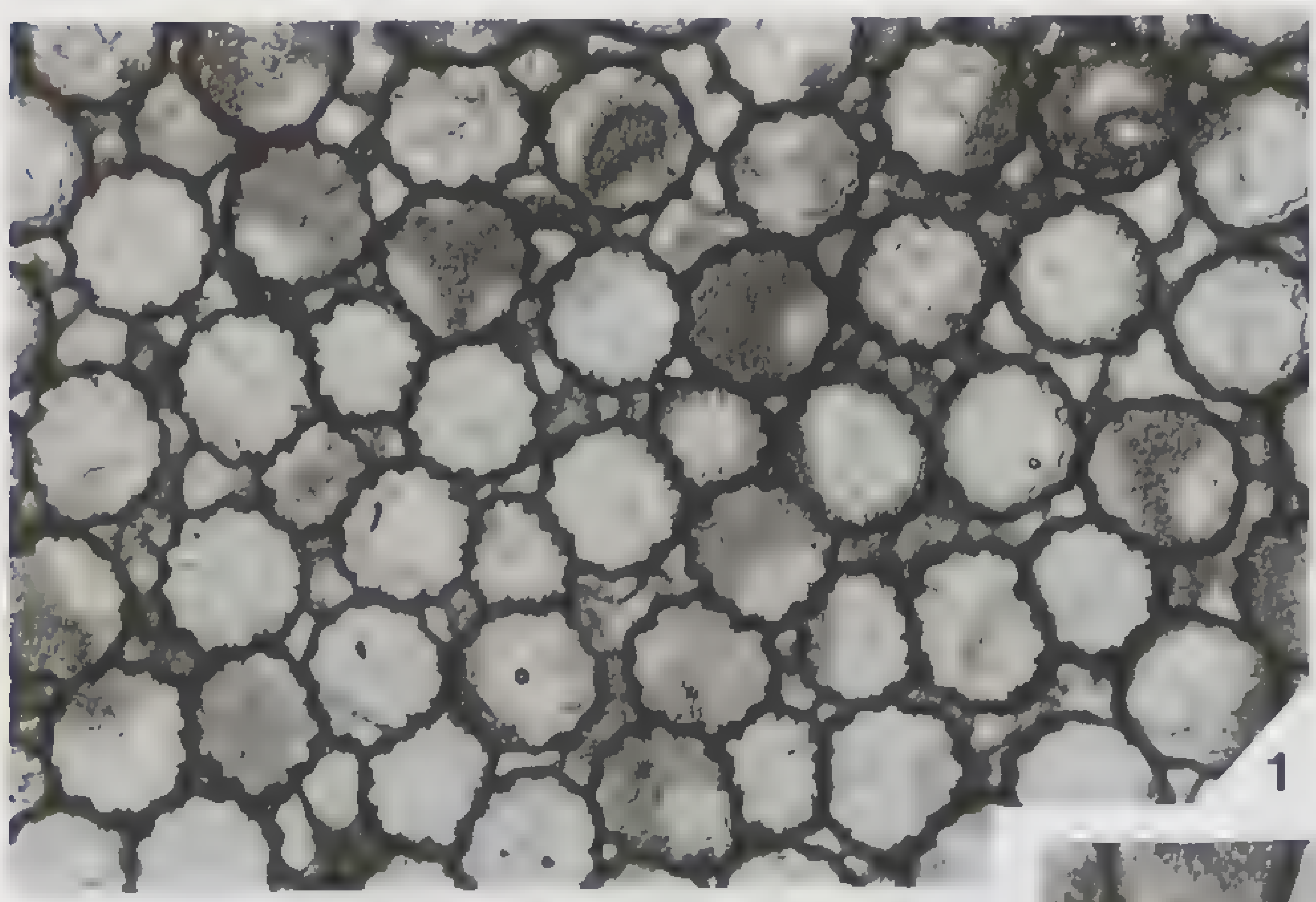
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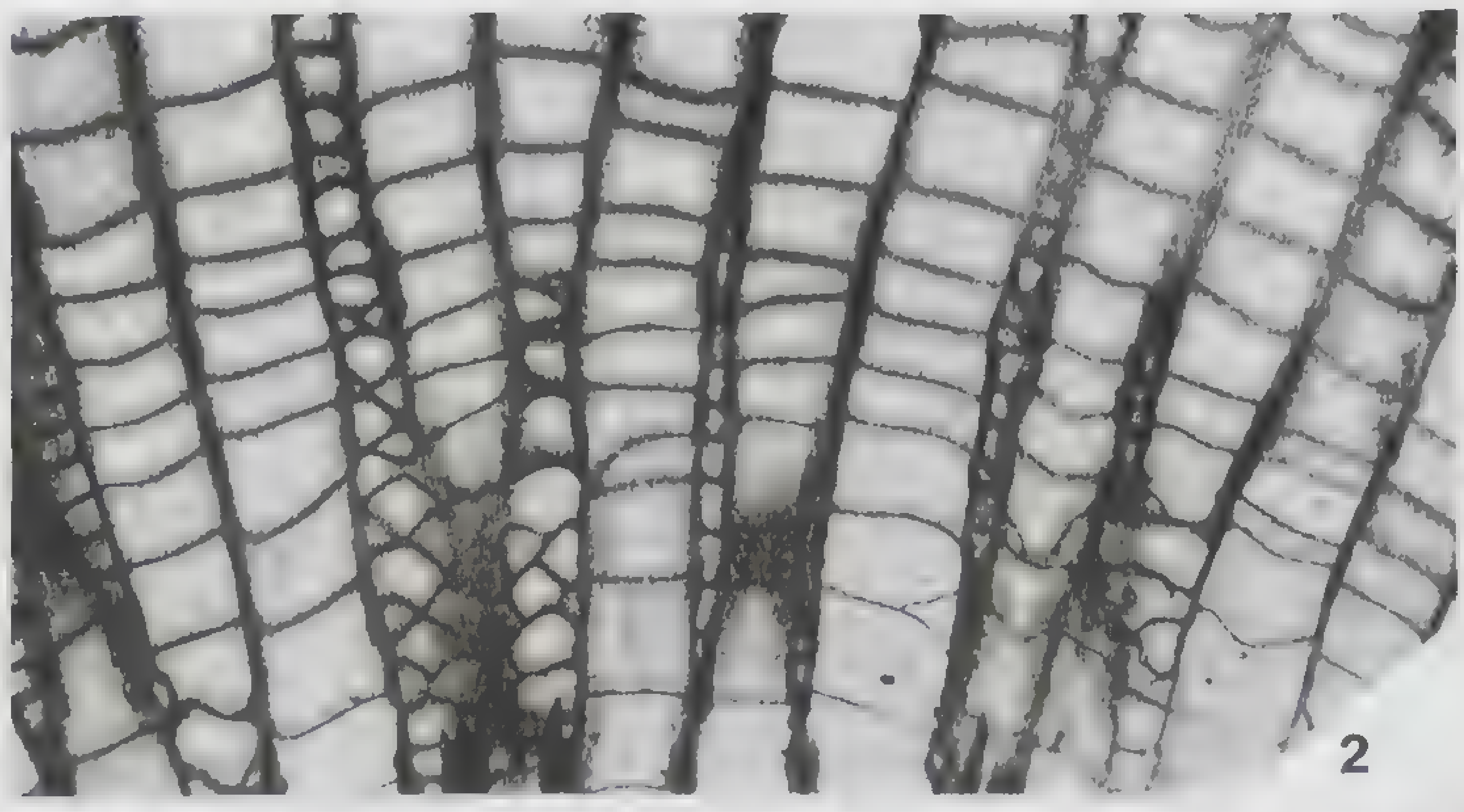
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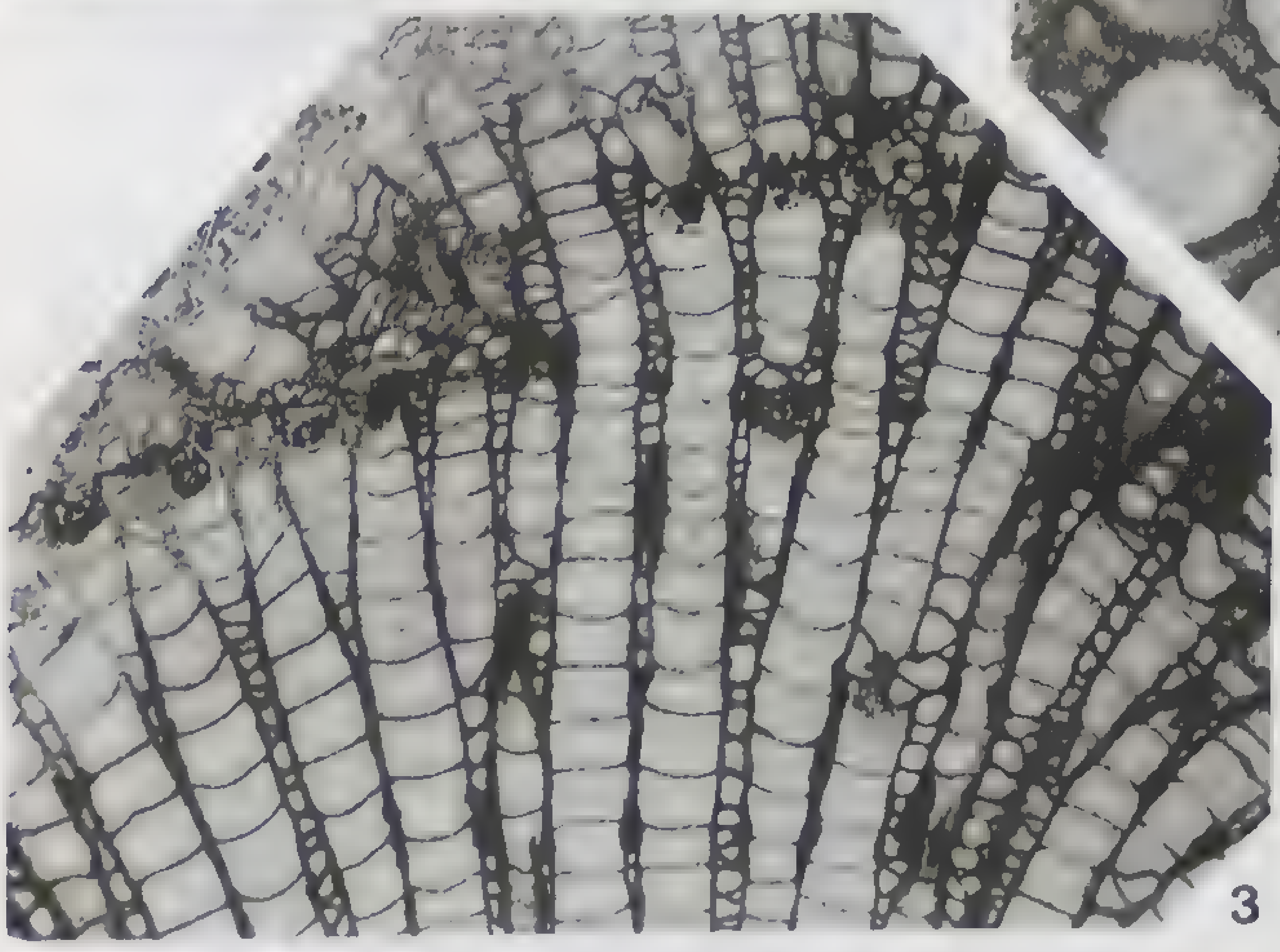
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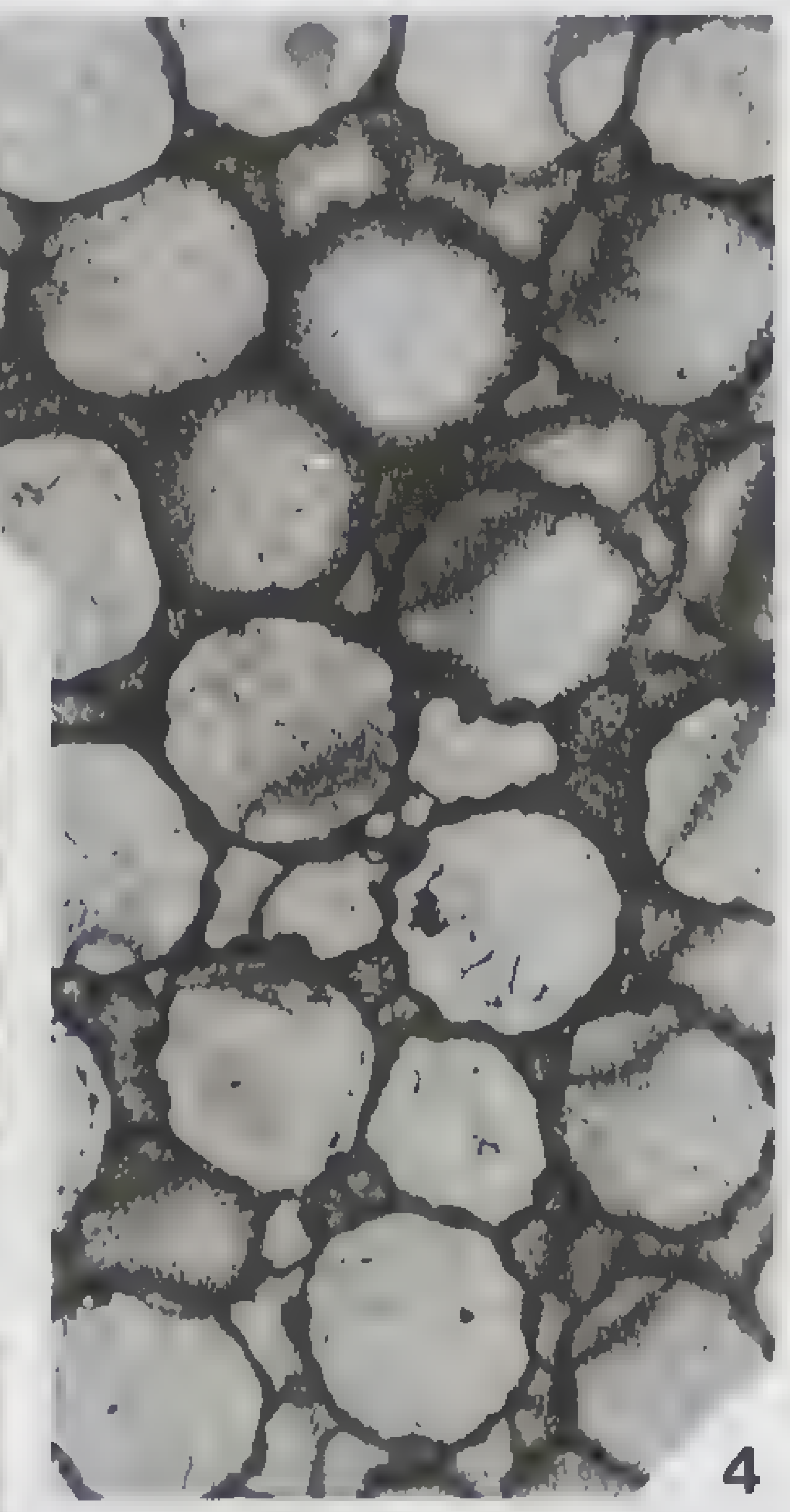
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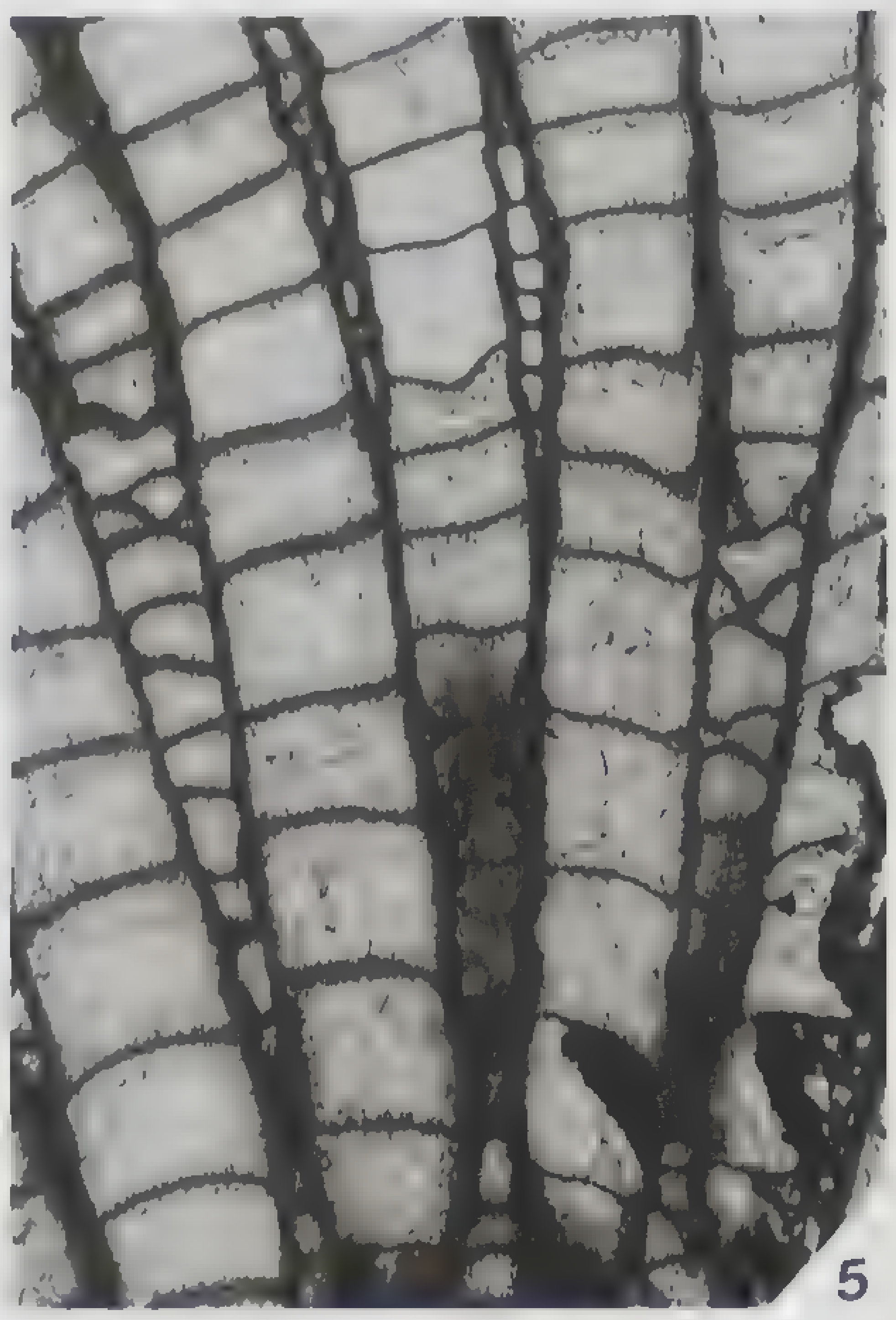
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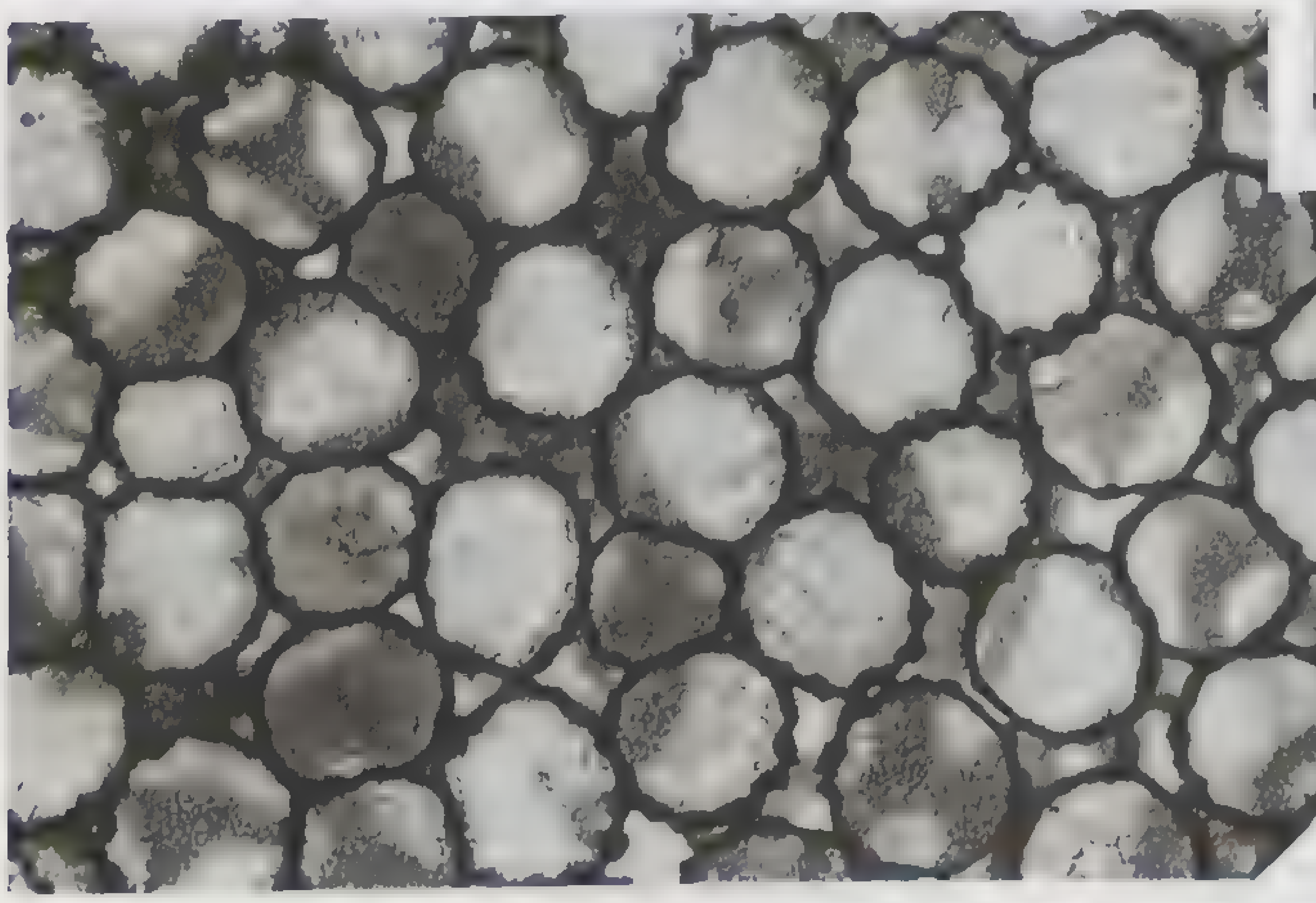
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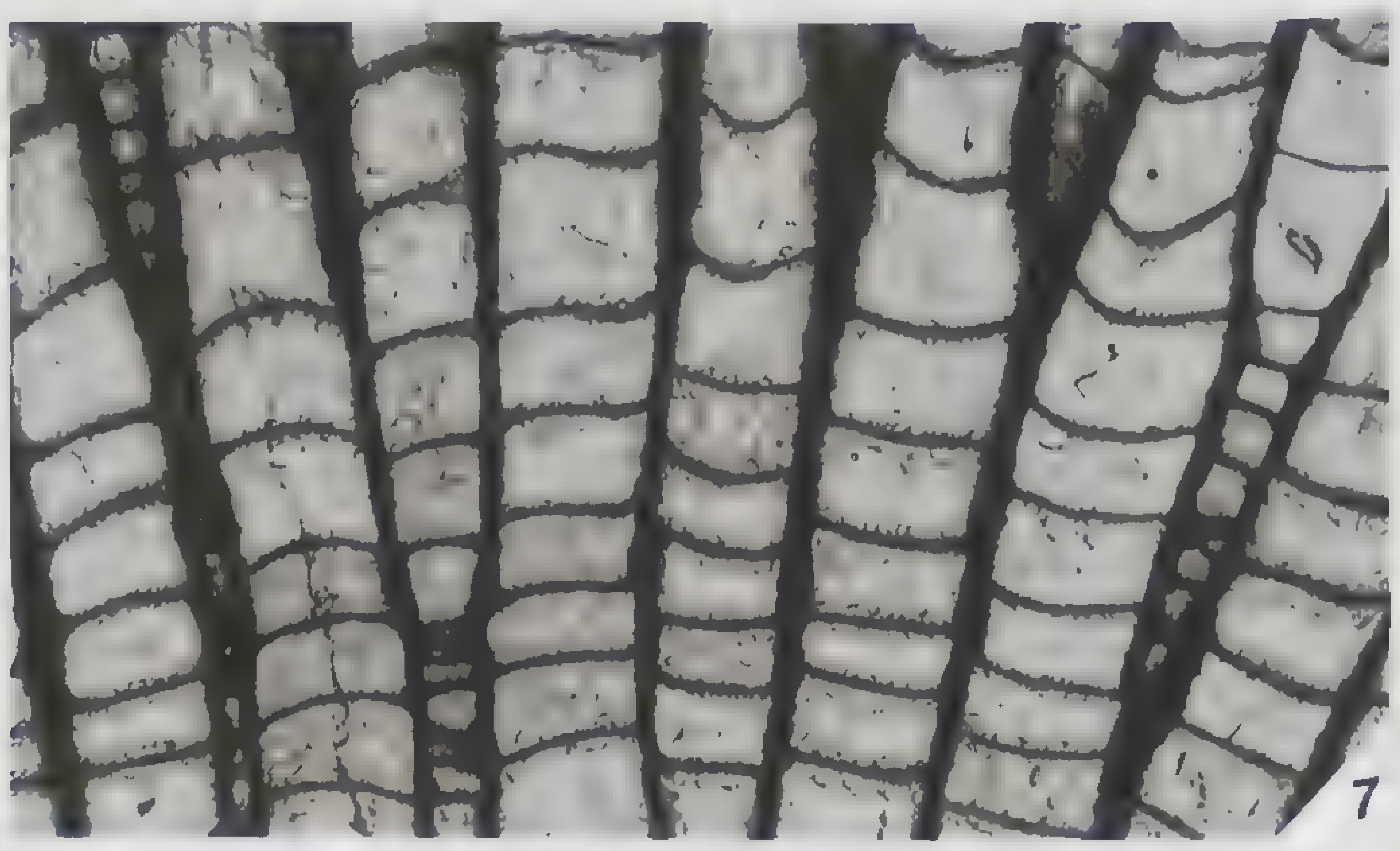
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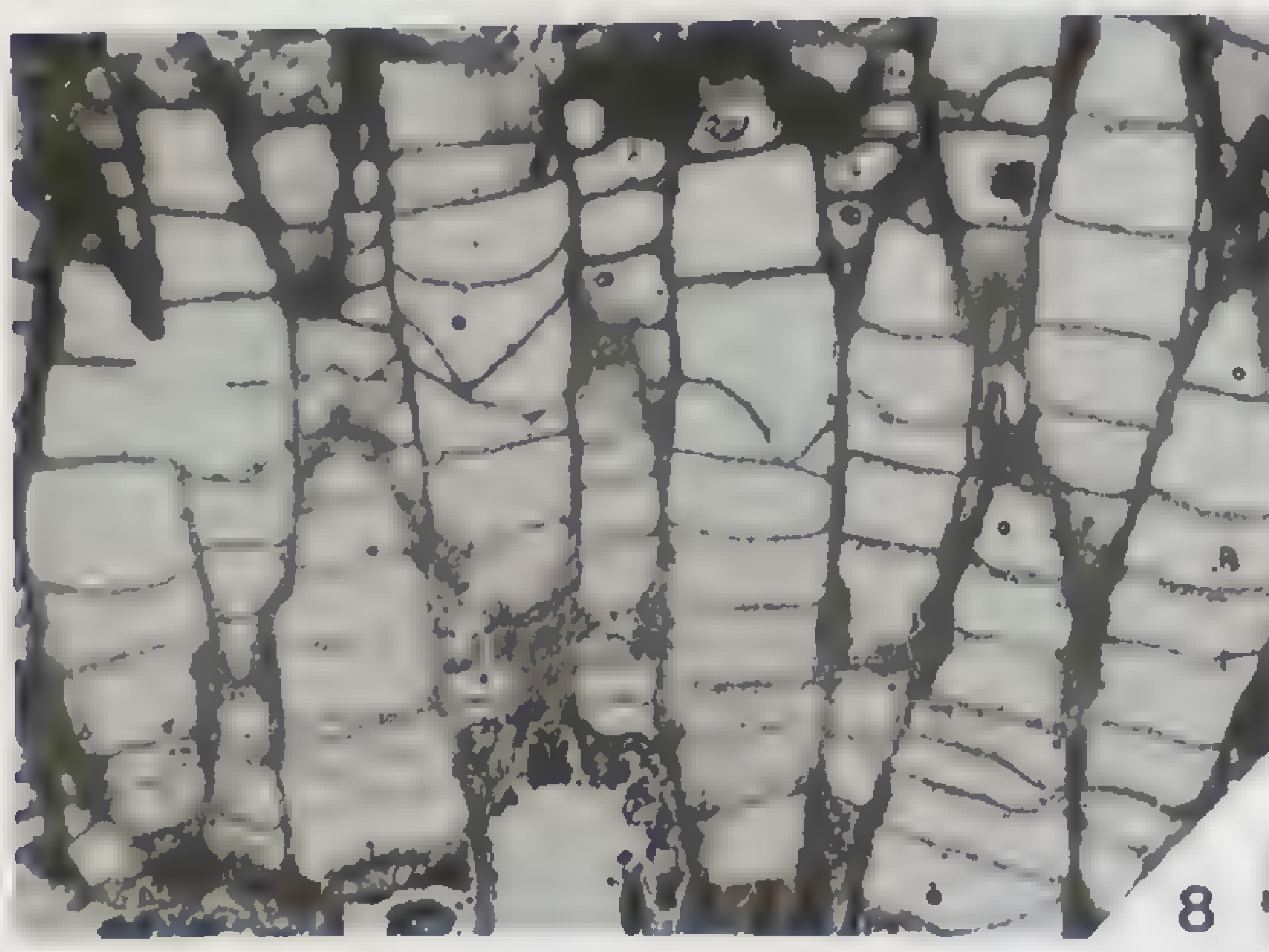
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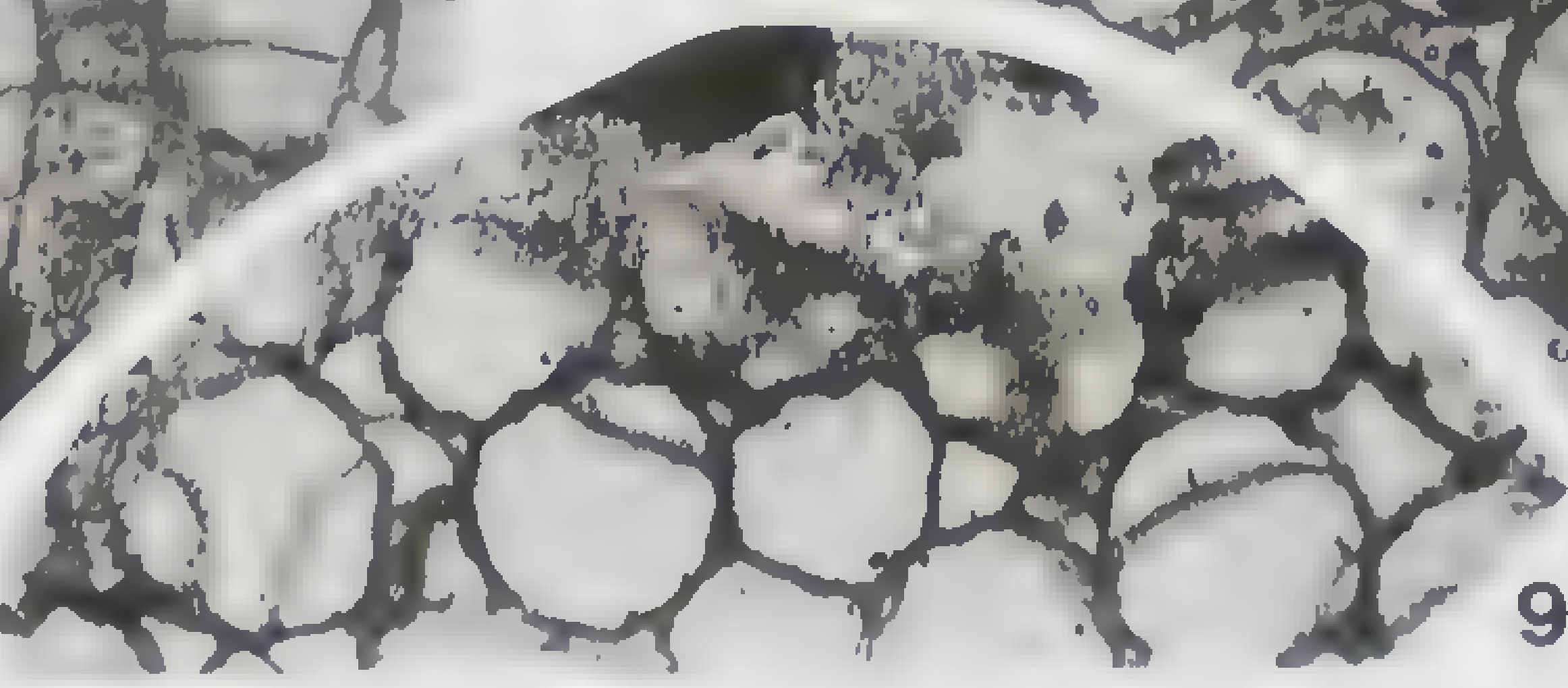
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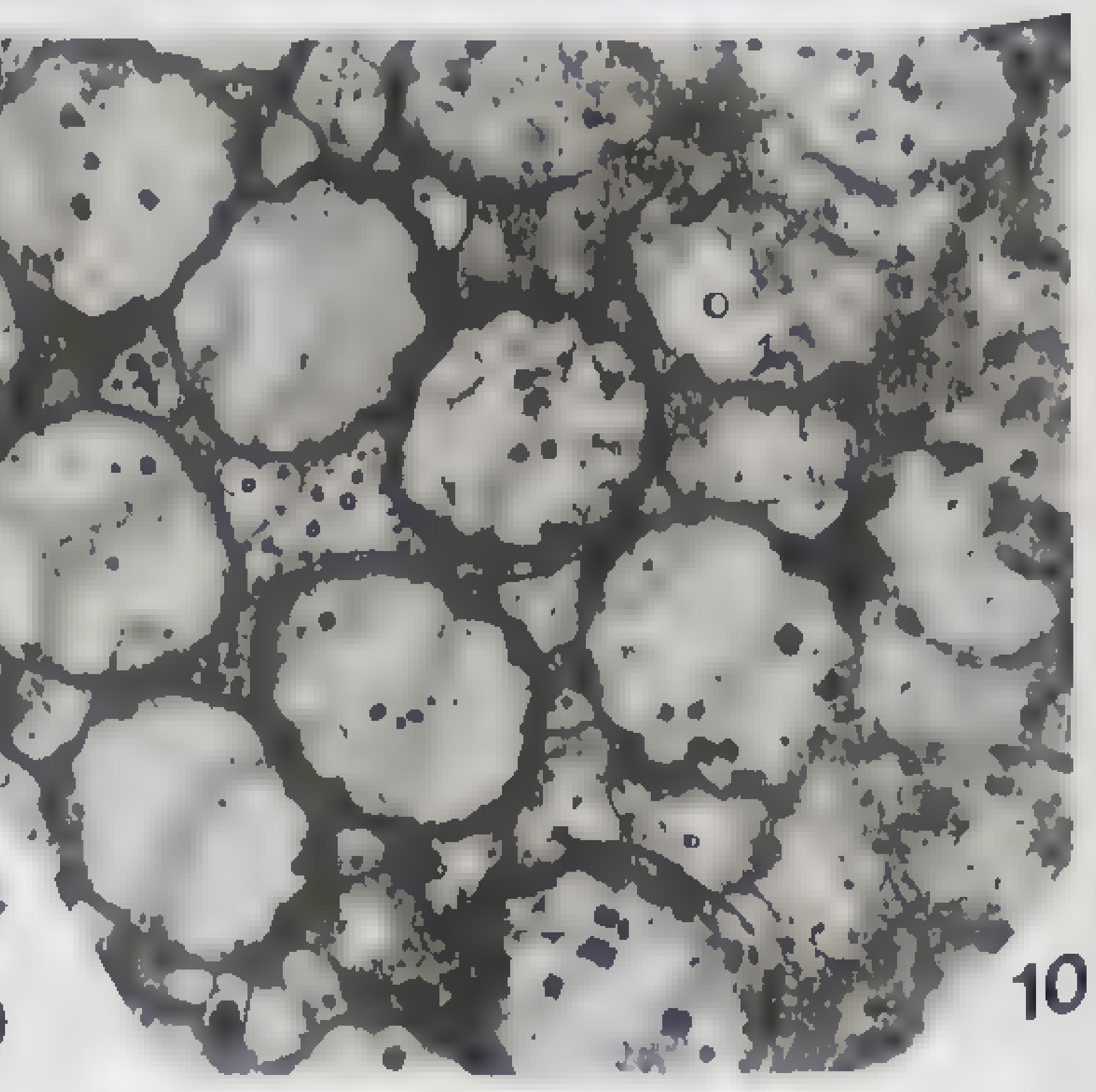
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EXPLANATION OF PLATE 4

Figure Page

1–10. ***Propora thebesensis*** (Foerste, 1909) 45

[1, 2, Kissenger Limestone Member, Bryant Knob Formation, Section-interval 15-1 (Calumet); 3–7, Kissenger Limestone Member, Bryant Knob Formation, Section-interval 14-1 (Higginbotham Farm); 8, coral-rich bedding surface of Mosalem Formation, Section-interval 32-1z (Thomson East); 9, 10, upper Mosalem Formation, Section-interval 32-1c (Thomson East).]

1, 2. USNM 485729: 1, transverse section, ×8; 2, longitudinal section, ×8.
3. USNM 485754: longitudinal section showing partial mortality and regeneration, ×5.
4, 5. USNM 485755: 4, transverse section, ×8; 5, longitudinal section, ×8.
6, 7. USNM 485753: 6, transverse section, ×8; 7, longitudinal section, ×8.
8. USNM 485758: longitudinal section, ×8.
9. USNM 485760: transverse section, ×8.
10. USNM 485762: transverse section, ×8.

EXPLANATION OF PLATE 5

Figure Page

1–10. ***Propora savagei,*** new species 56

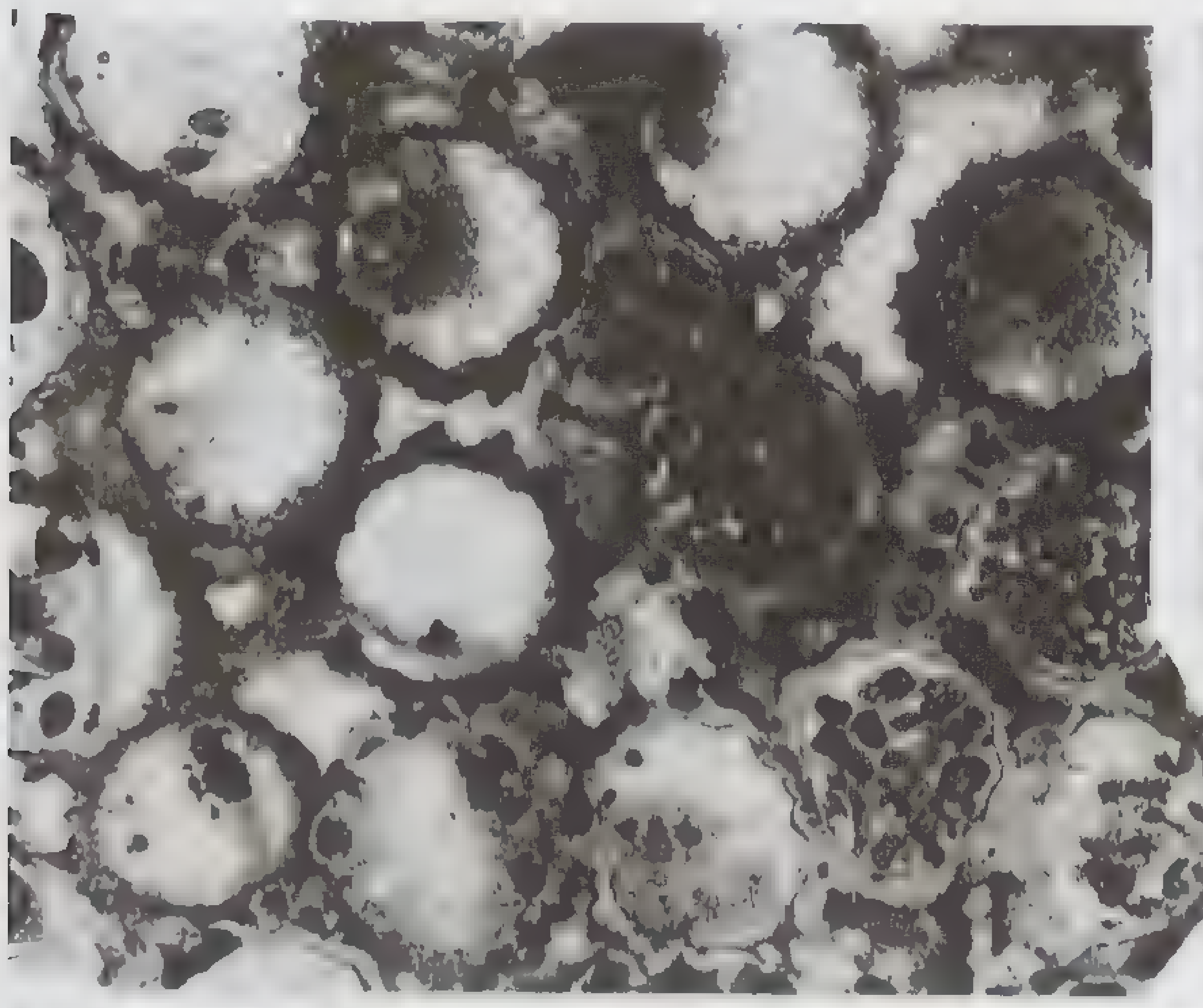
[1–3, oölite of Keel Formation, Section-interval 23-3 (Lawrence Quarry) (site 23ii); 4, Leemon Formation, Section-interval 31-1 (Thebes North); 5, 6, Leemon Formation (undivided), Section 31 (Thebes North); 7–10, Leemon Formation, Section-interval 20-6 (Short Farm).]

1–3. USNM 485764 (paratype): 1, transverse section, ×8; 2, longitudinal section, ×8; 3, longitudinal section through a tabularium, ×20.

4. USNM 485769: longitudinal section, ×8.

5, 6. UI X-8722 (holotype): 5, transverse section, ×8; 6, longitudinal section showing sediment inclusion and rejuvenescence, ×8.

7–10. USNM 485766 (paratype): 7, transverse section, ×40; 8, longitudinal section showing regeneration in a composite corallum, ×8; 9, transverse section, ×8; 10, longitudinal section, ×8.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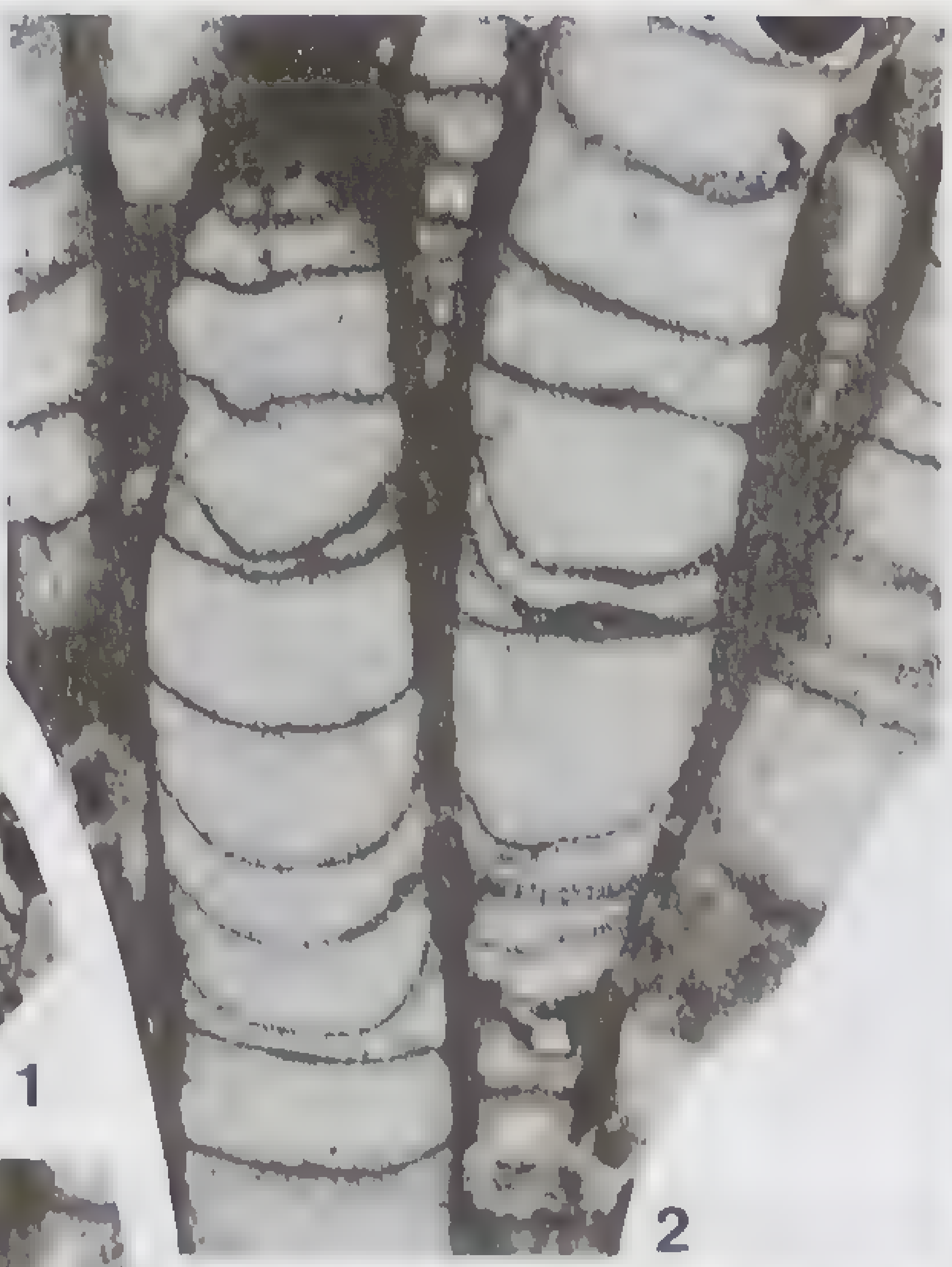
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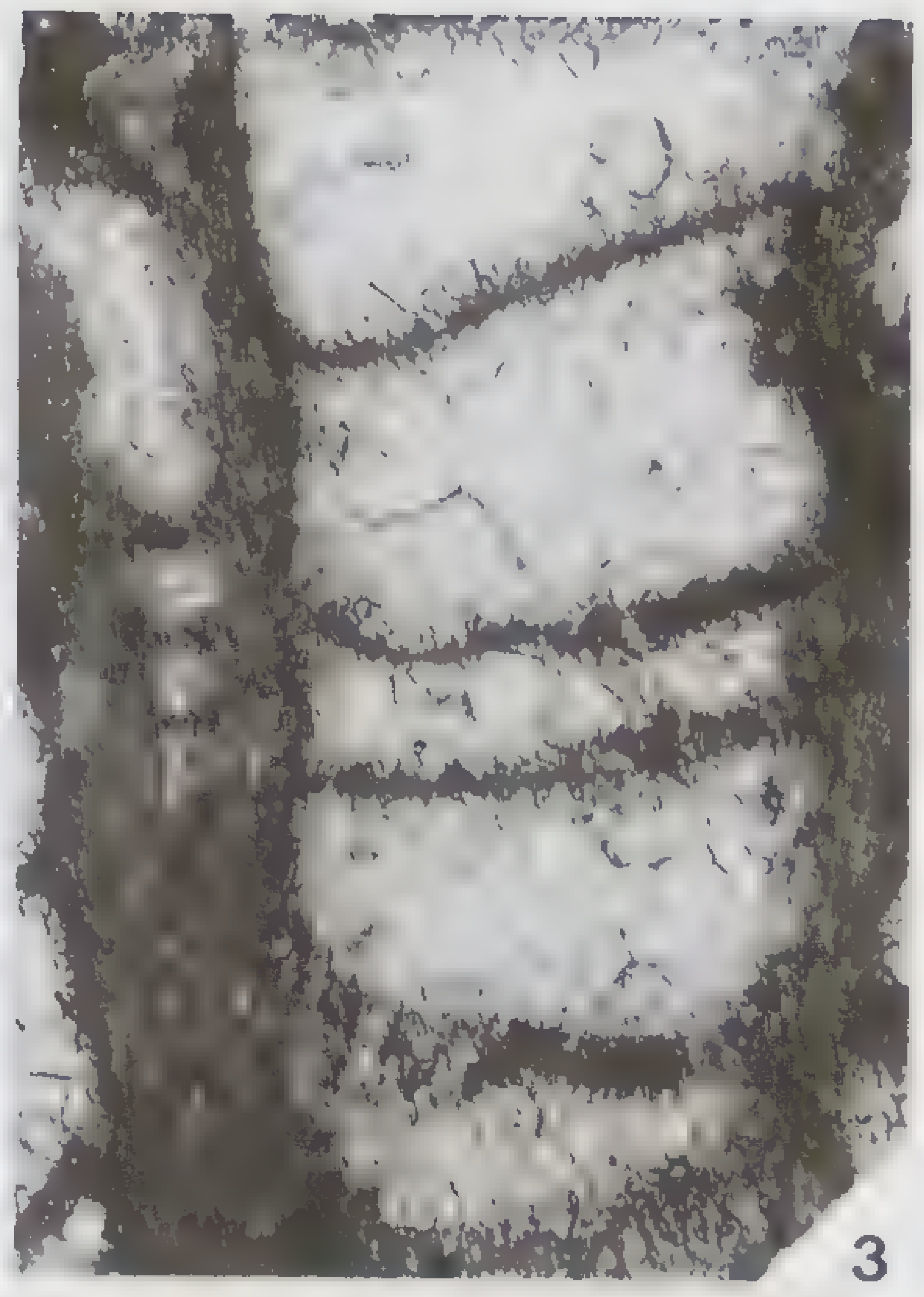
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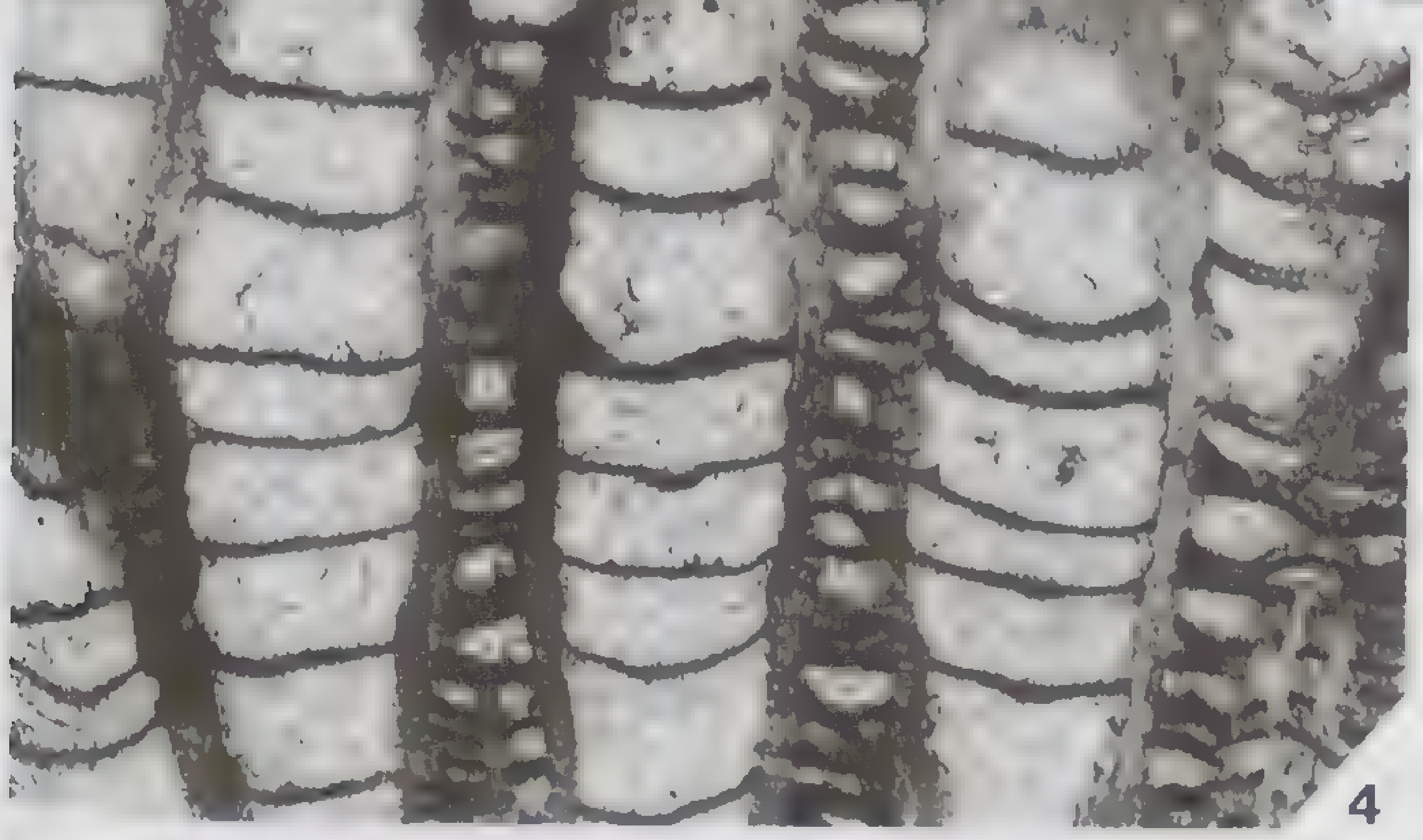
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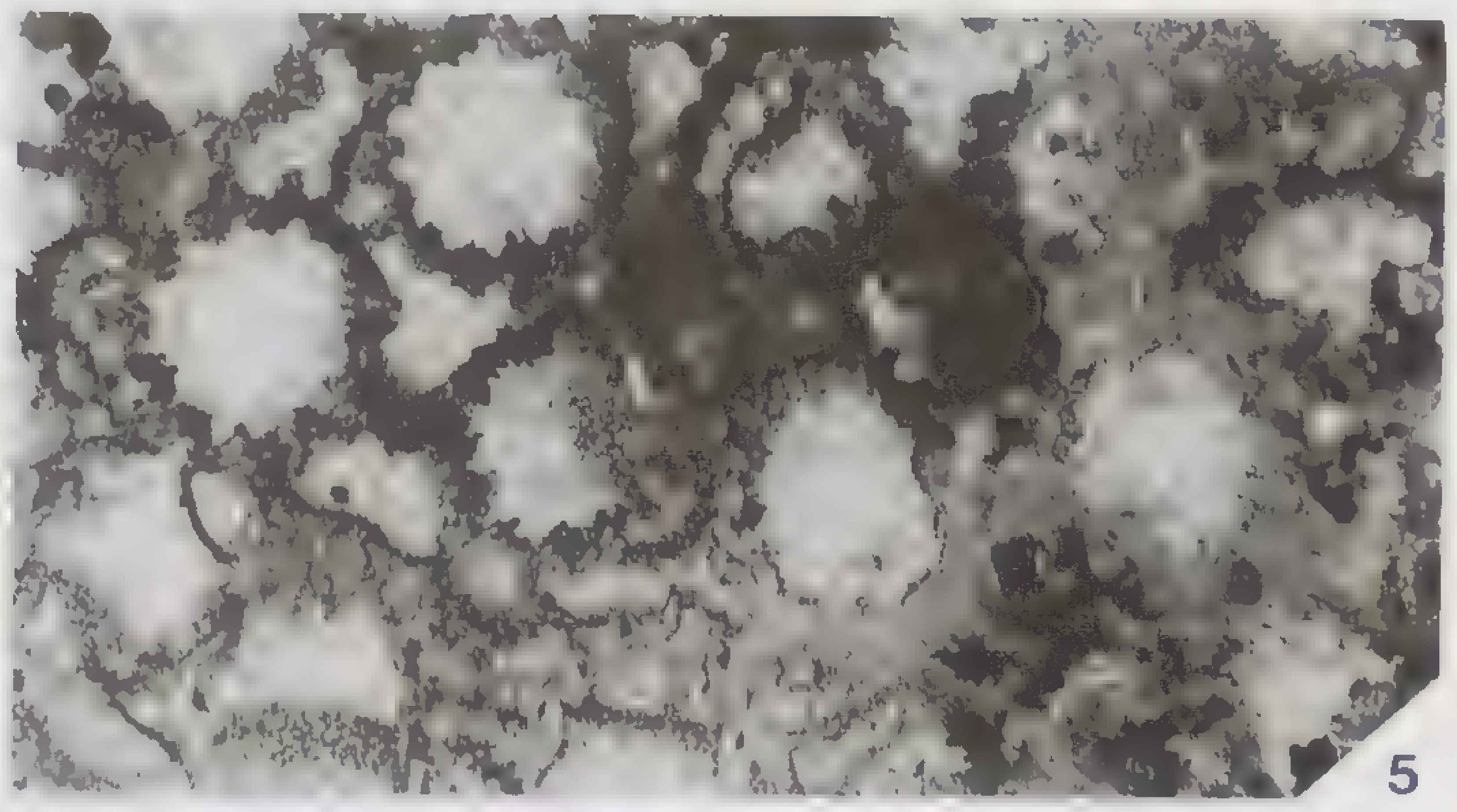
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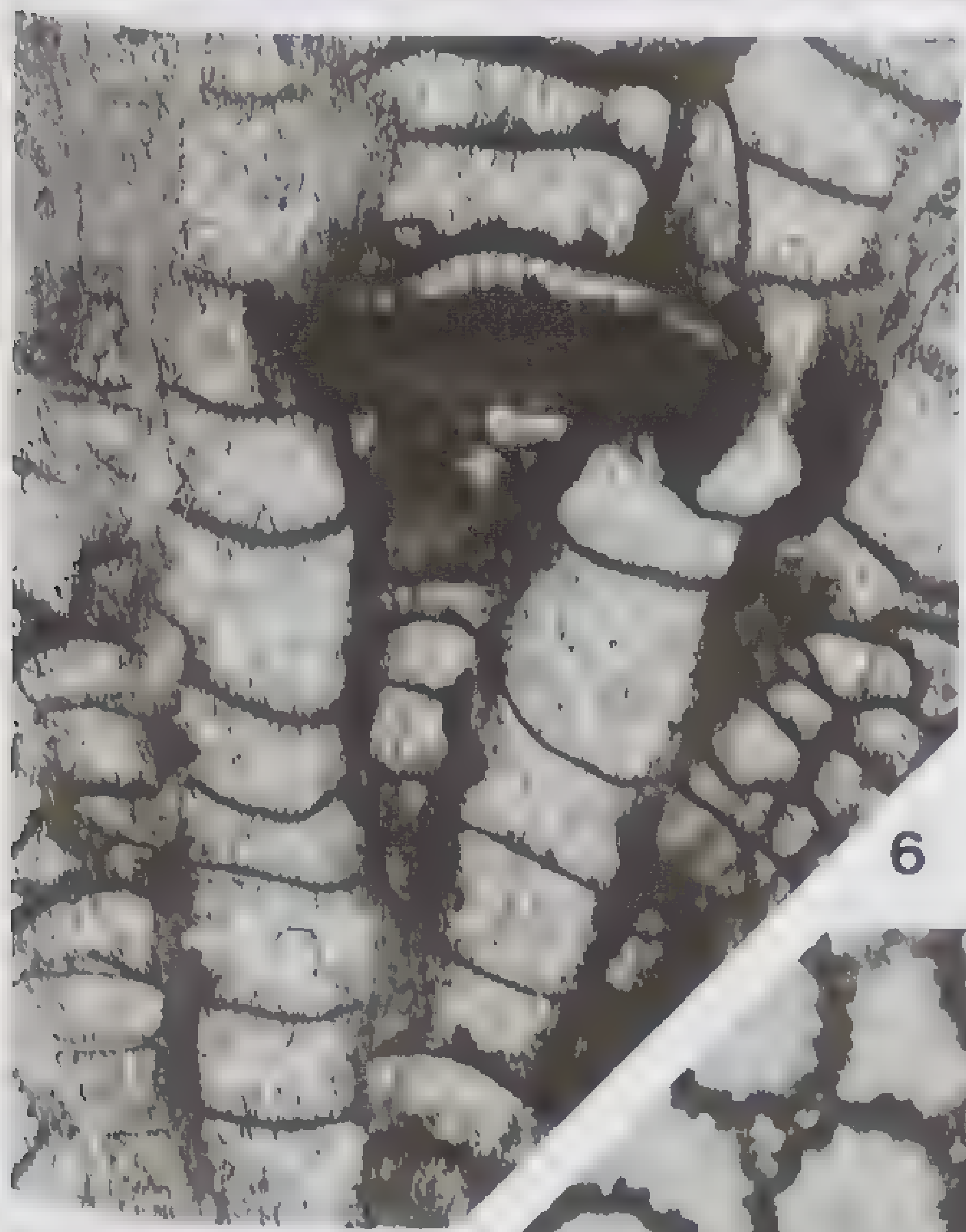
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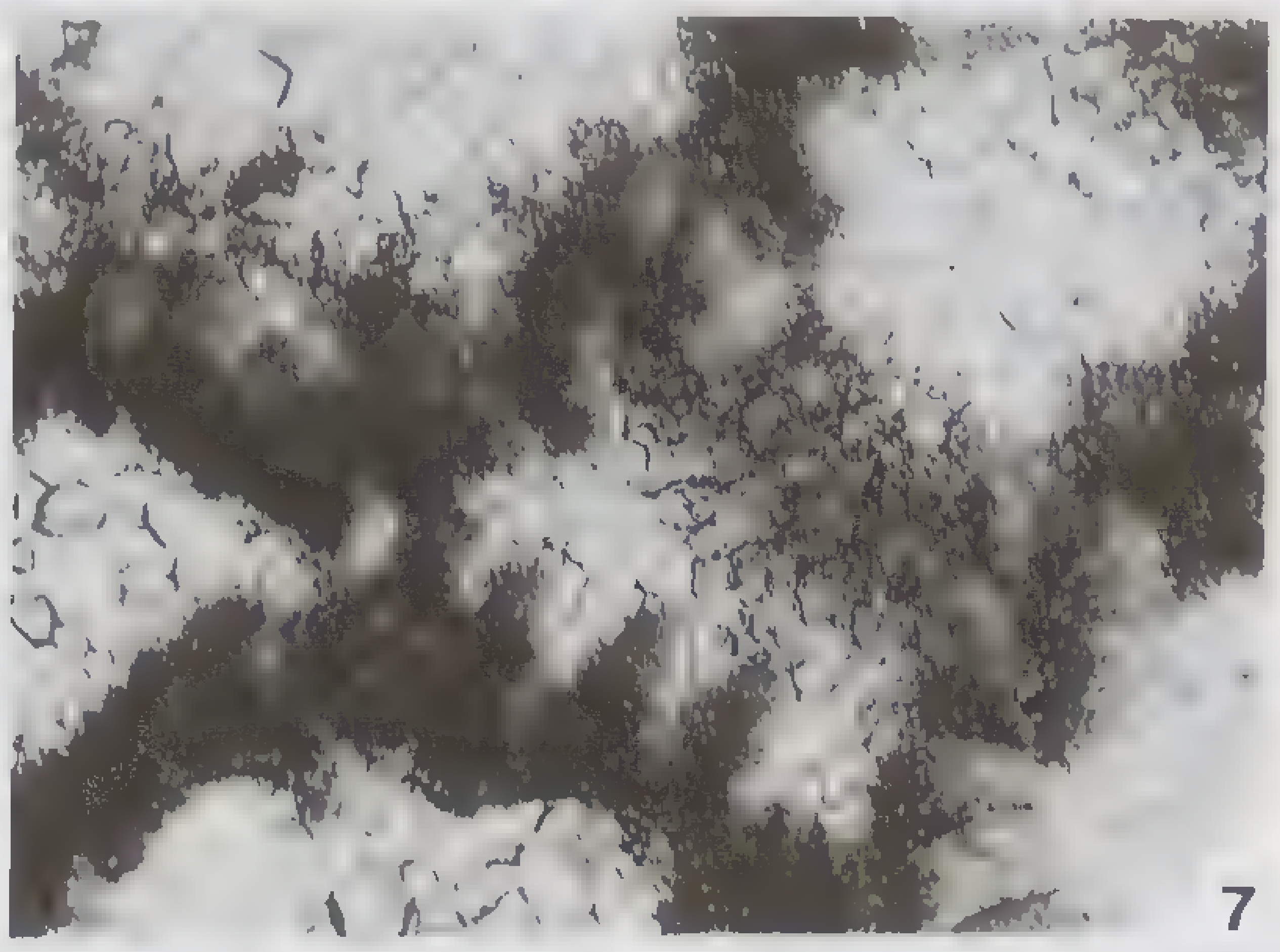
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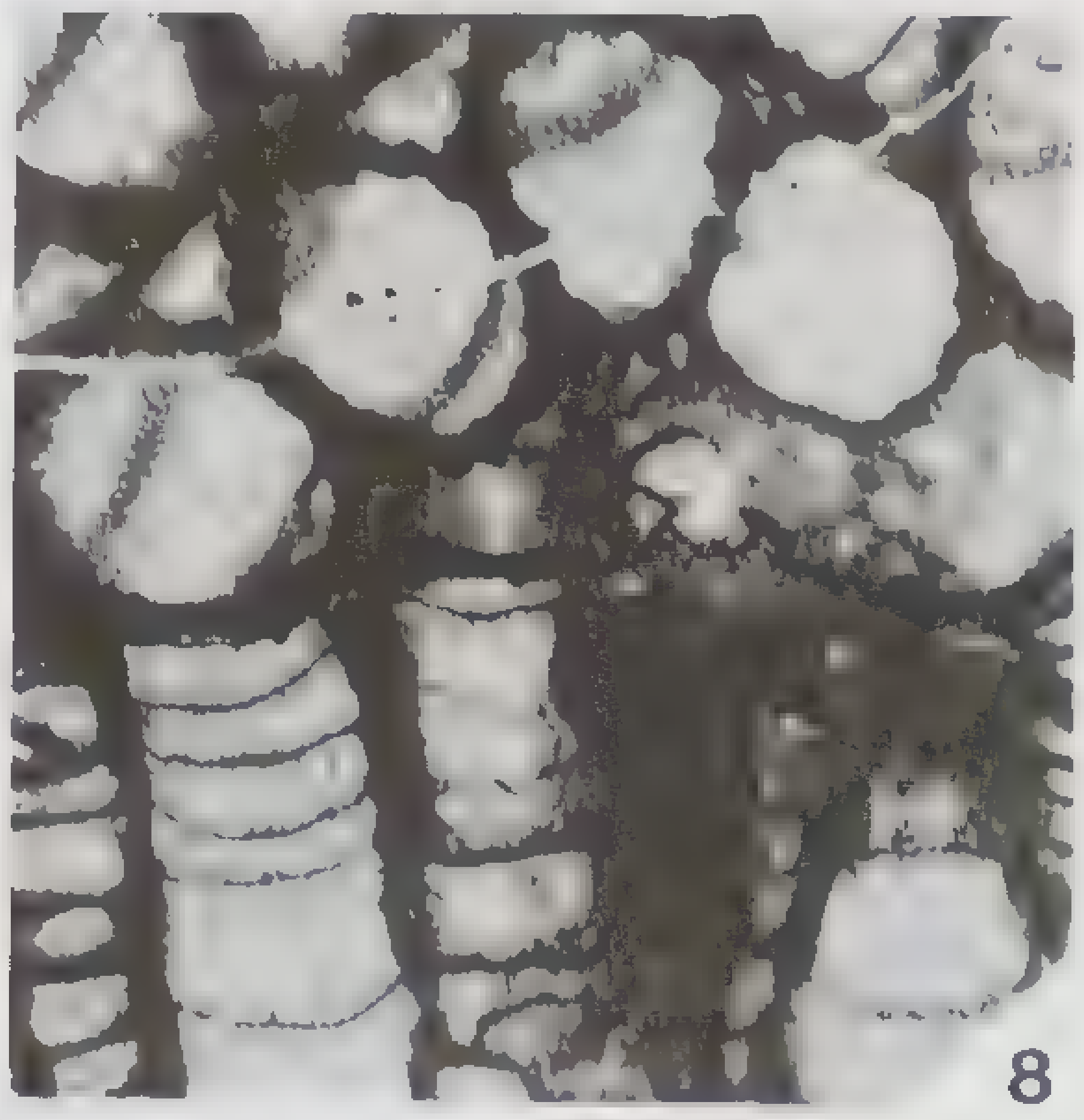
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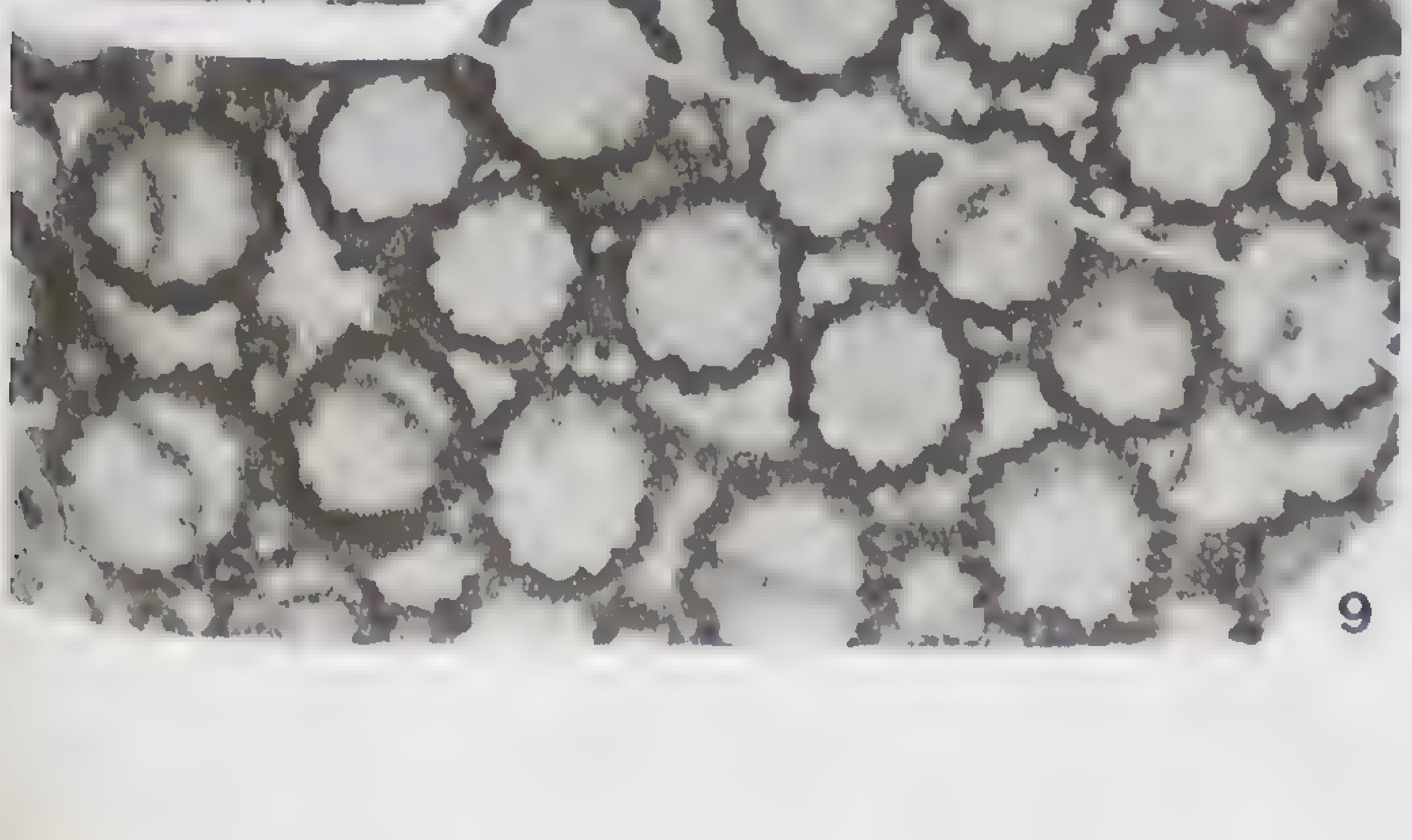
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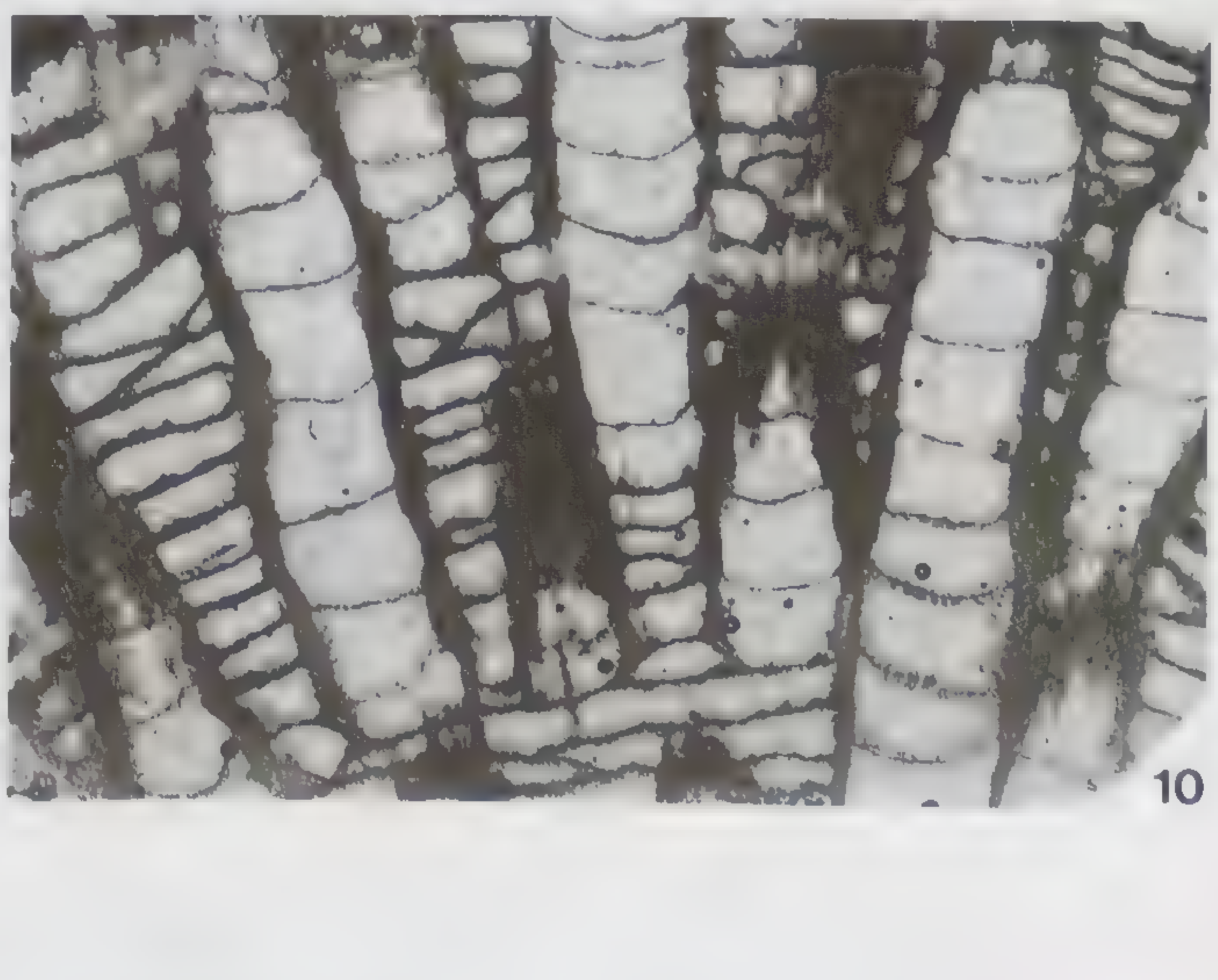
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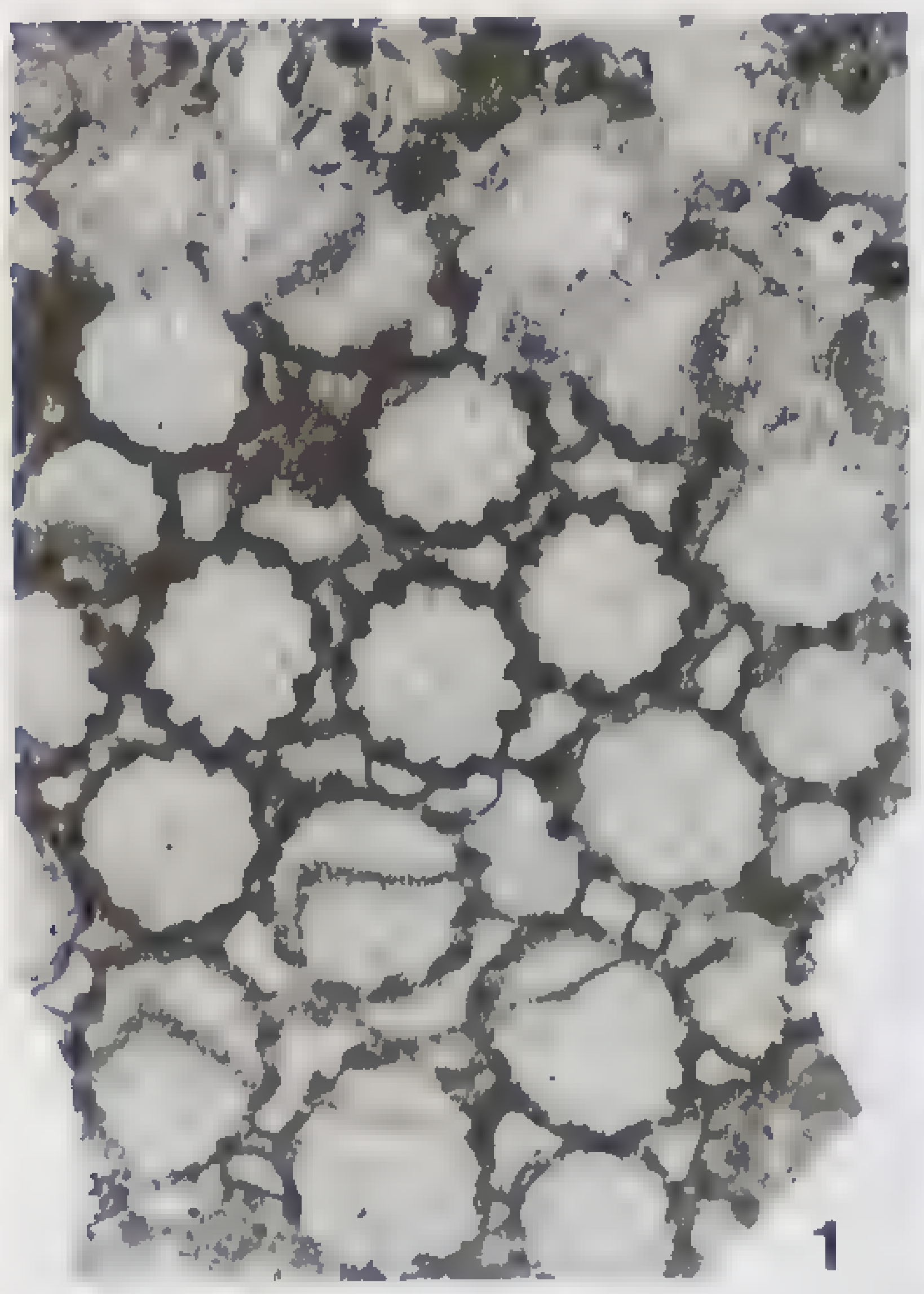
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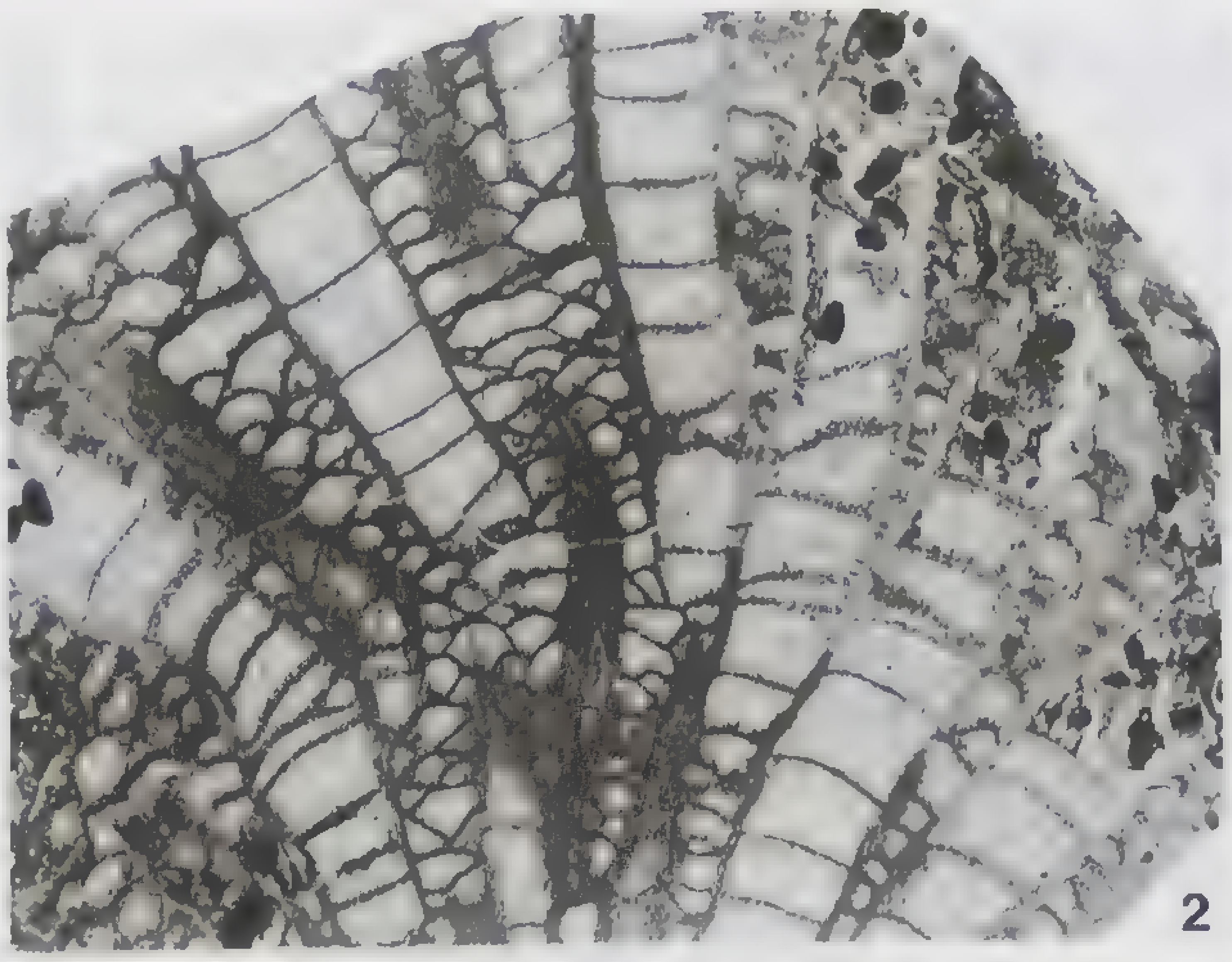
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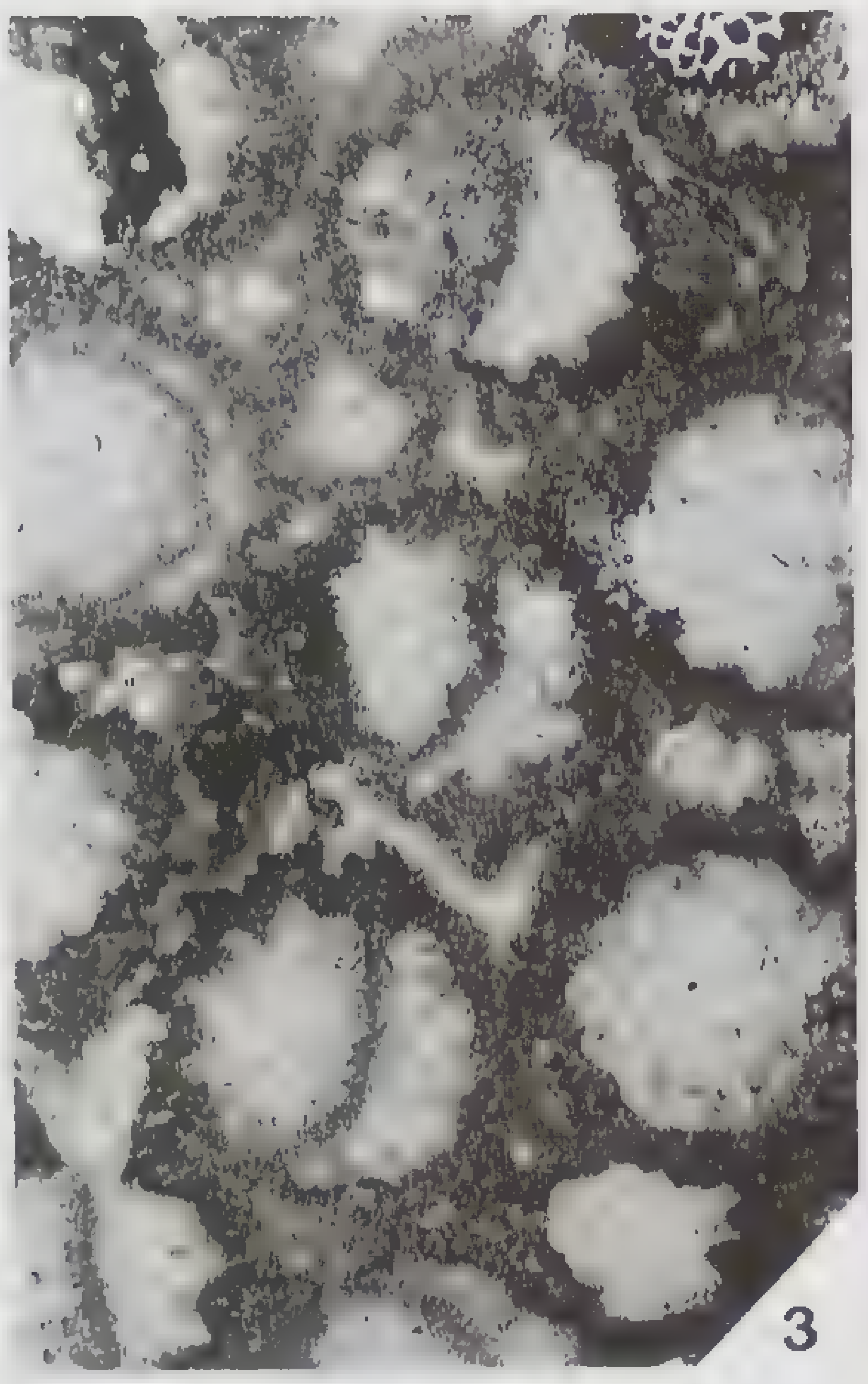
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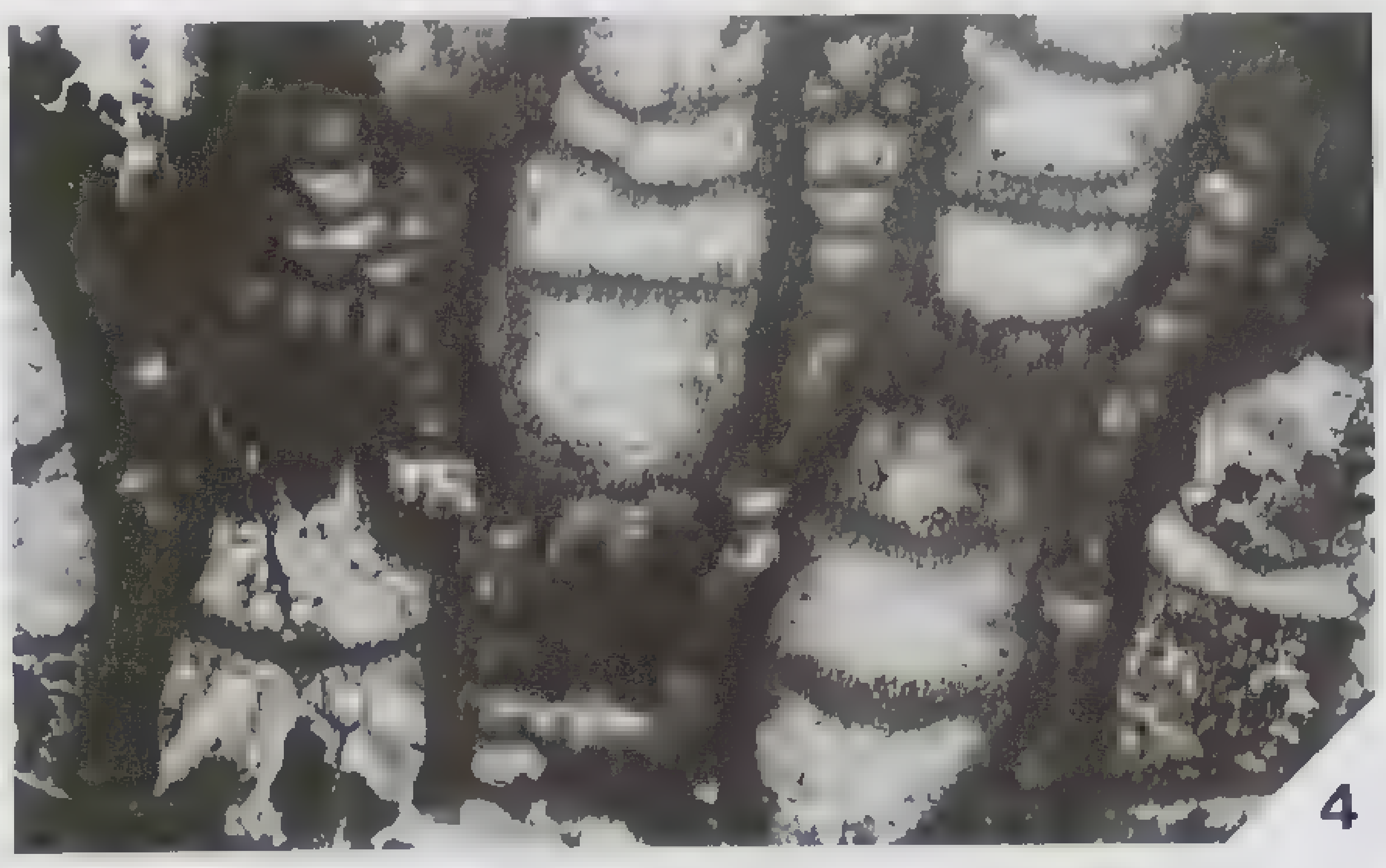
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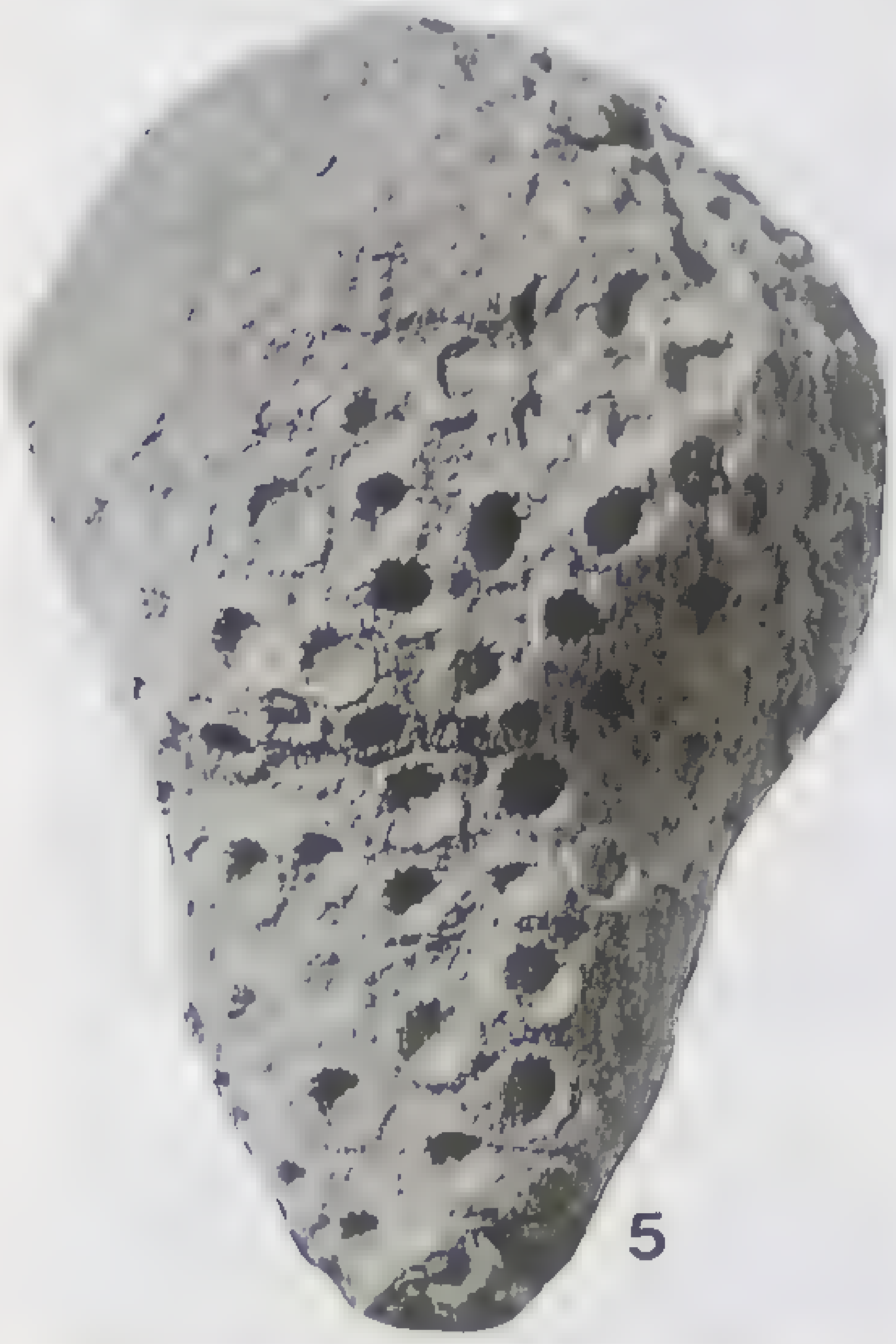
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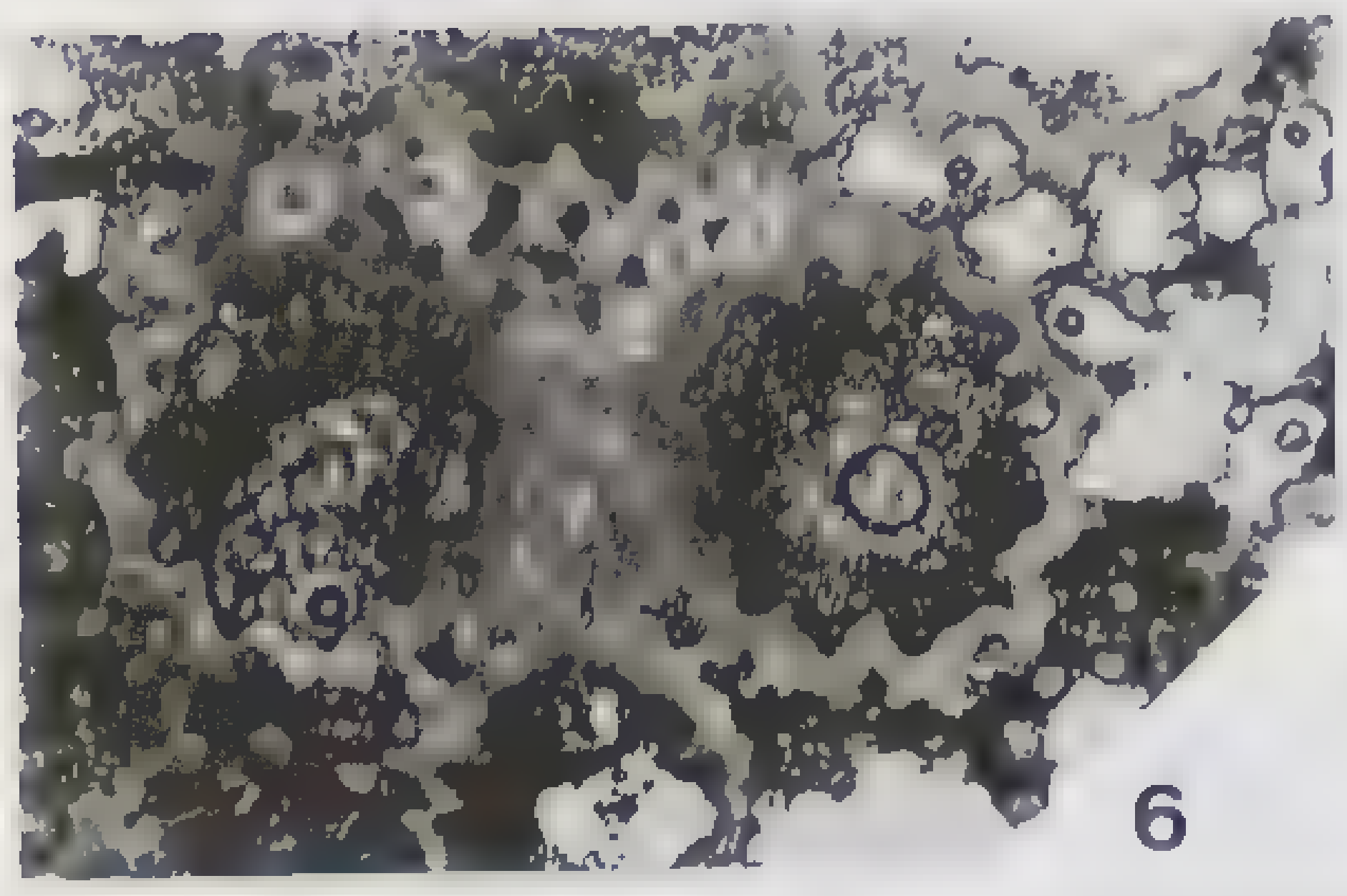
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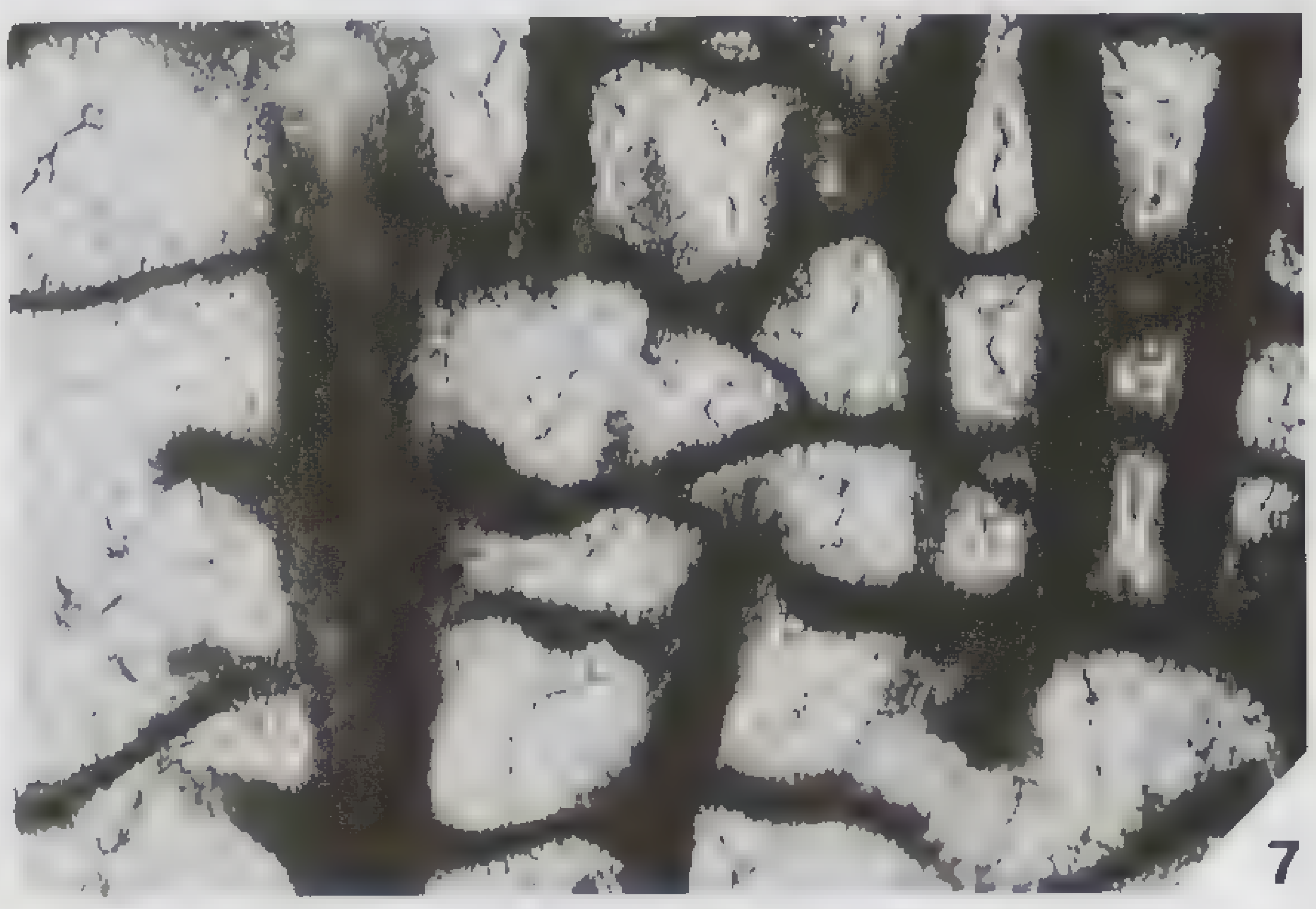
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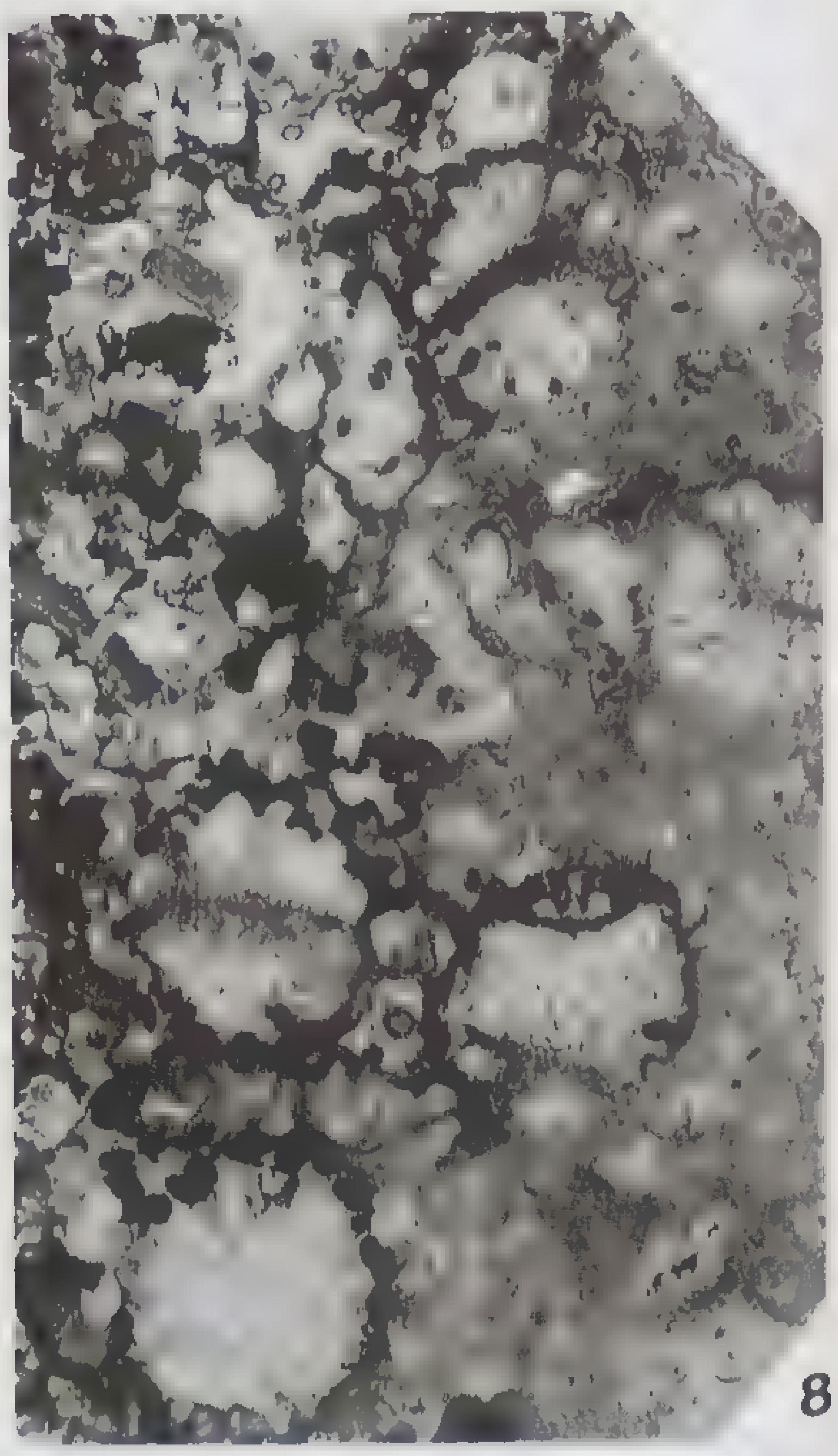
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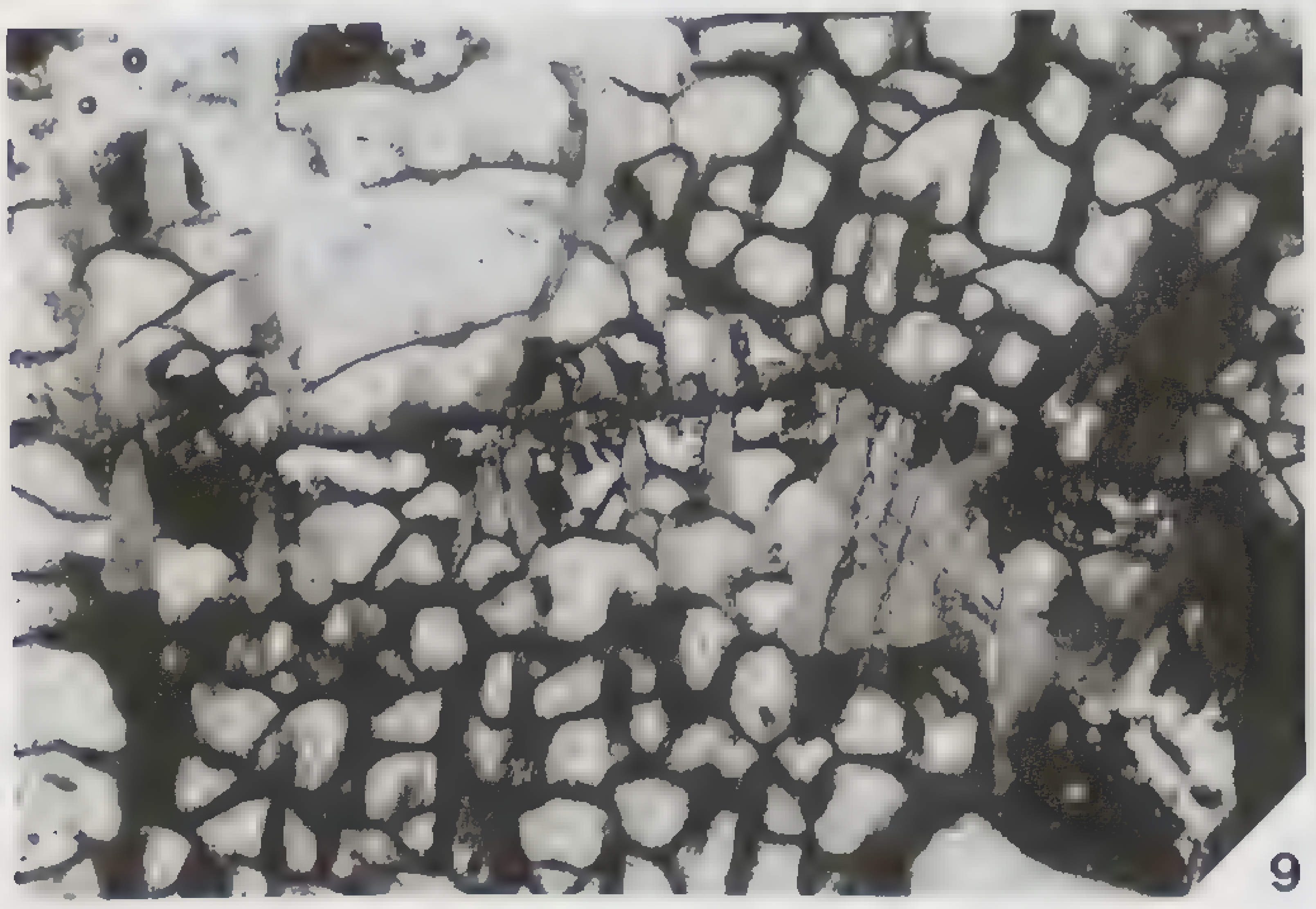
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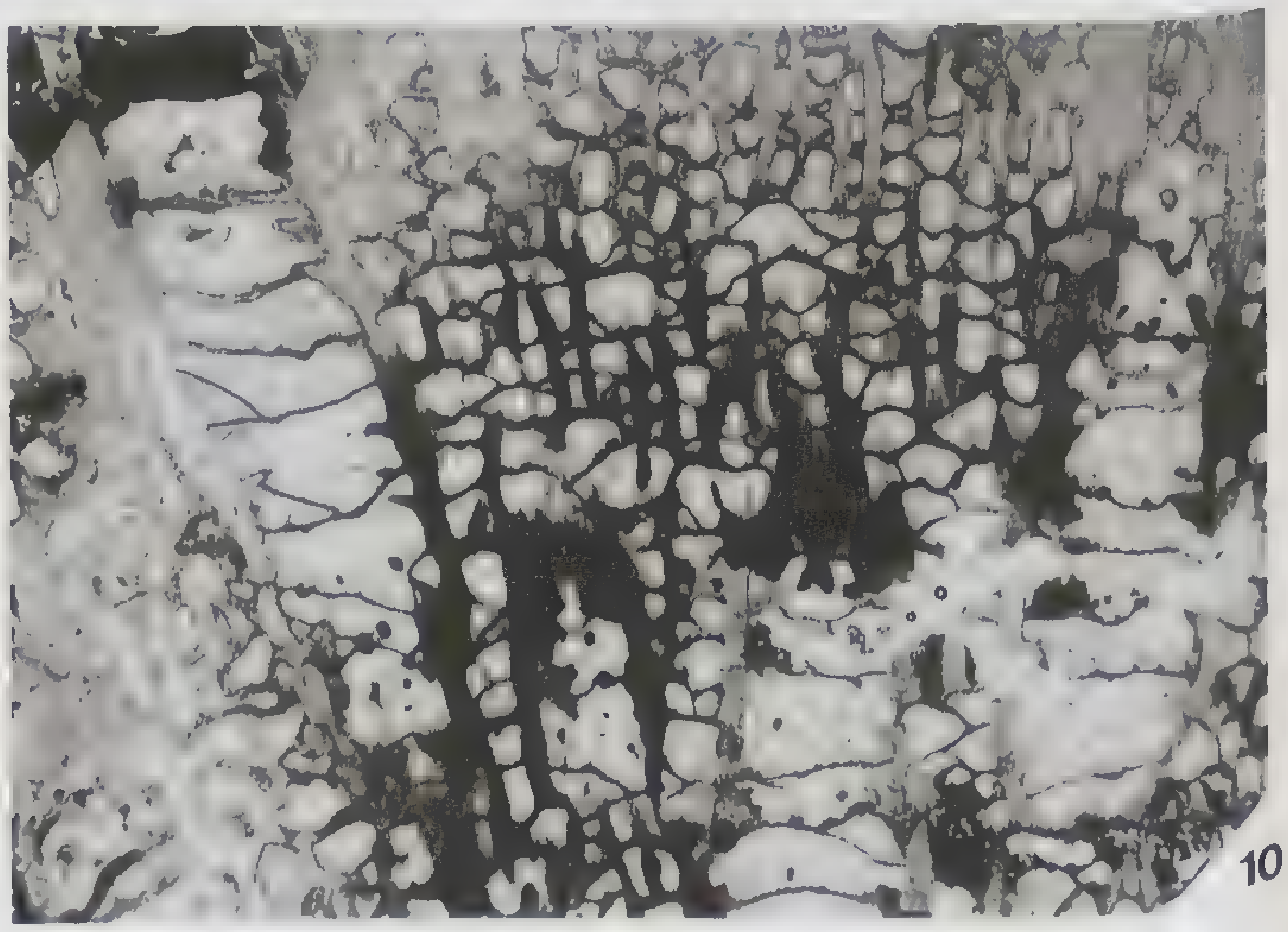
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EXPLANATION OF PLATE 6

Figure Page

1–4. ***Propora savagei,*** new species 56

[1, 2, Leemon Formation, Section-interval 20-1 (Short Farm); 3, 4, Kissenger Limestone Member, Bryant Knob Formation, Section-interval 14-1 (Higginbotham Farm).]

1, 2. USNM 485765 (paratype): 1, transverse section, ×8; 2, longitudinal section, ×8.

3, 4. USNM 485775: 3, transverse section, ×8; 4, longitudinal oblique section, ×8.

5–10. ***Propora speciosa*** (Billings, 1865) 58

[5, Ellis Bay Formation, White Cliff, Anticosti Island, Québec; 6–10, Leemon Formation, Section 31 (Thebes North).]

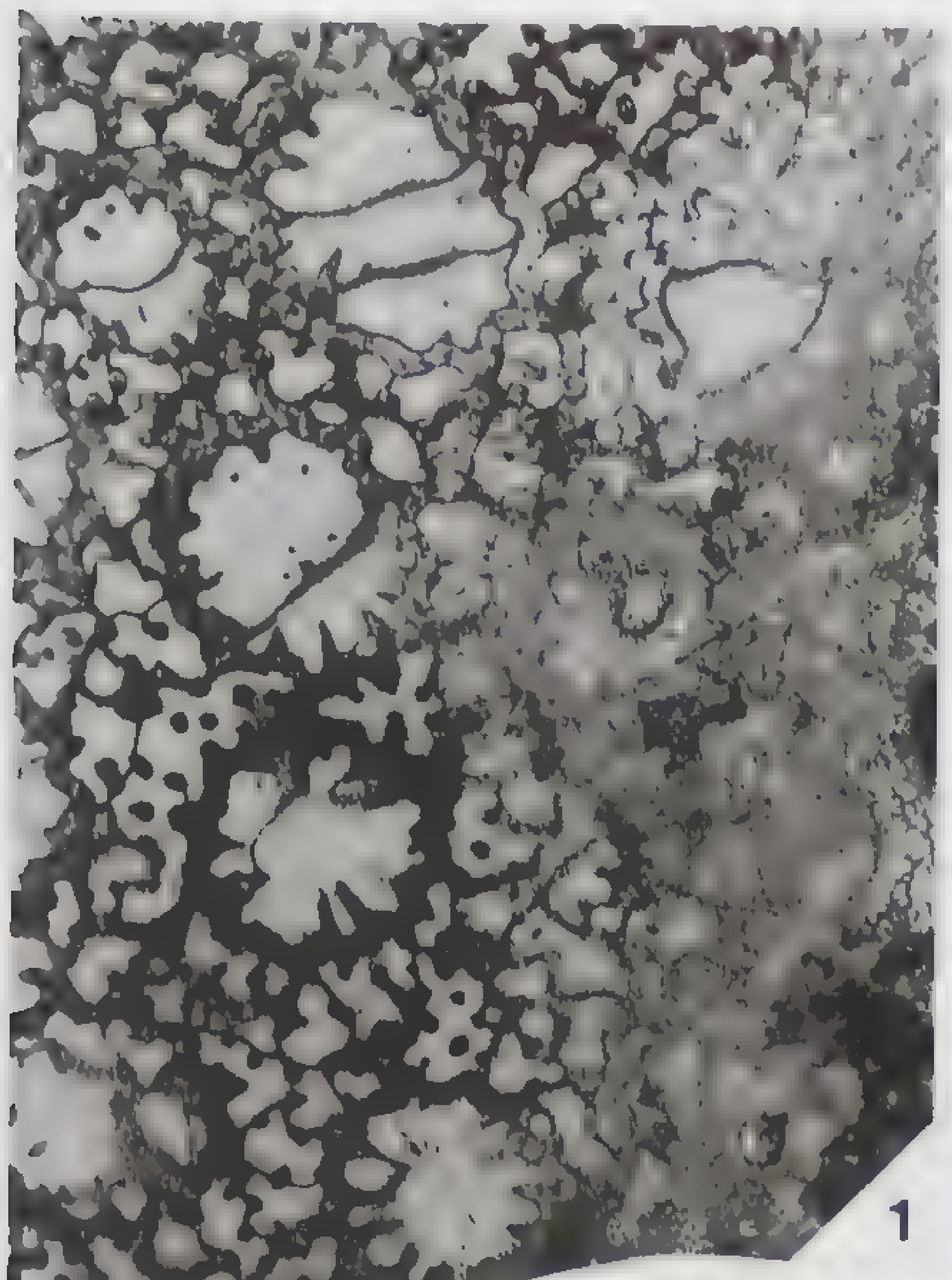
5. GSC 2240a (lectotype): exterior lateral view of corallum, ×1.5.

6. UI C-1438: transverse section, ×5.

7–10. UI C-889a: 7, longitudinal section showing trabecular rods in coenenchyme (detail from left of center in 10, turned 20° clockwise), ×20; 8, transverse section, ×5; 9, longitudinal section showing regeneration, ×8; 10, longitudinal section, ×5.

EXPLANATION OF PLATE 7

Figure		Page
1–8.	***Propora speciosa*** (Billings, 1865)	58
	[1–7, Leemon Formation, Gale Section; 8, upper Mosalem Formation, Section-interval 32-1c (Thomson East).]	
1–6.	UI X-850: 1, transverse section, ×5; 2, longitudinal section, ×5; 3, transverse section (detail from lower left of center in 1, turned 180°), ×15; 4, transverse section (detail from top center in 3) showing septal structure, ×40; 5, exterior view of broken longitudinal surface, ×2; 6, exterior view of transverse surface, ×2.	
7.	UI C-1440: transverse section, ×5.	
8.	USNM 485776: transverse section, ×5.	
9, 10.	***Propora*** species aff. ***P. affinis*** (Billings, 1865)	62
	[Elwood Formation, Section-interval 29-4 (Sears Pit).]	
9, 10.	USNM 485777: 9, transverse section, ×8; 10, longitudinal section, ×8.	



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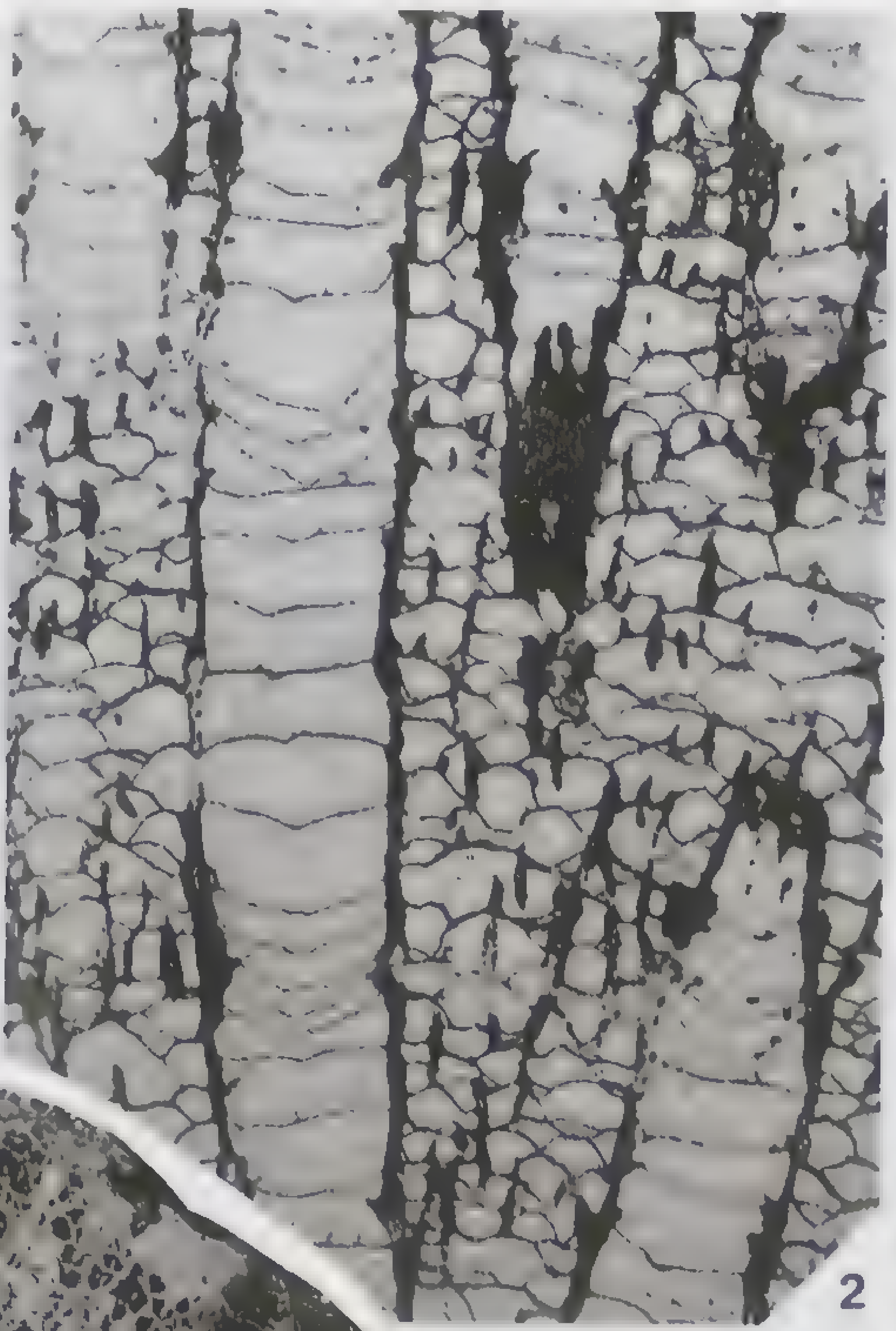

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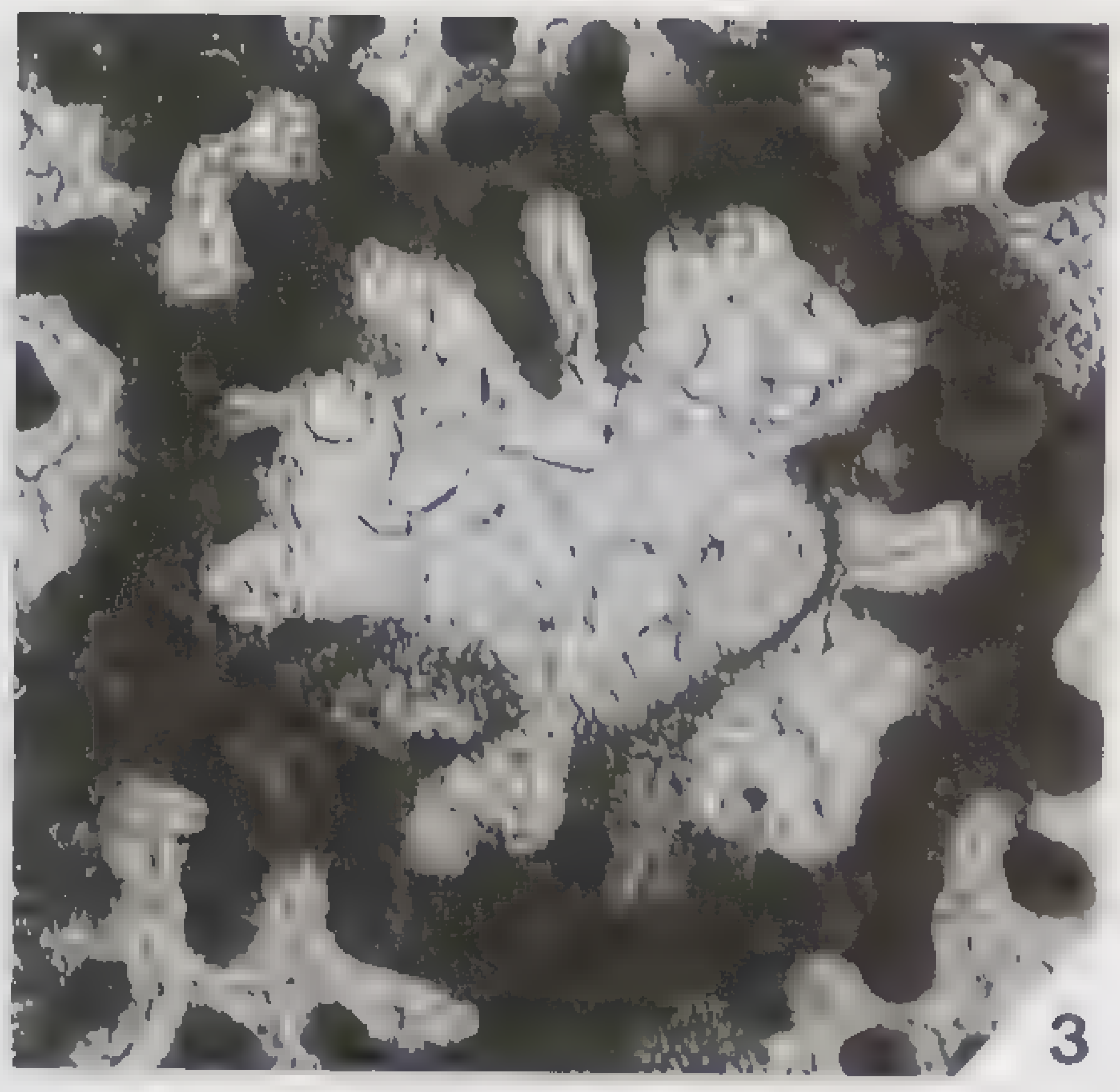

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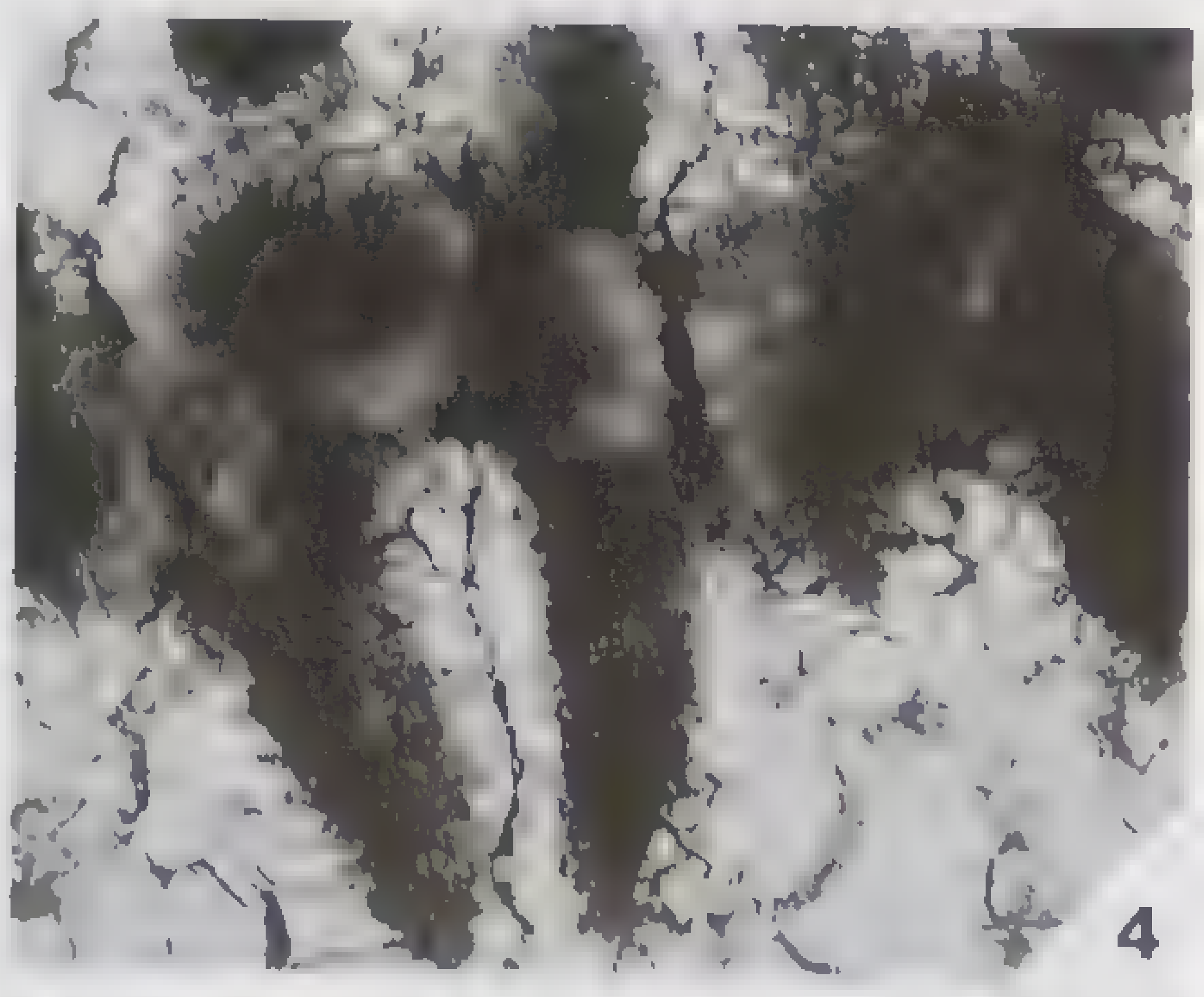

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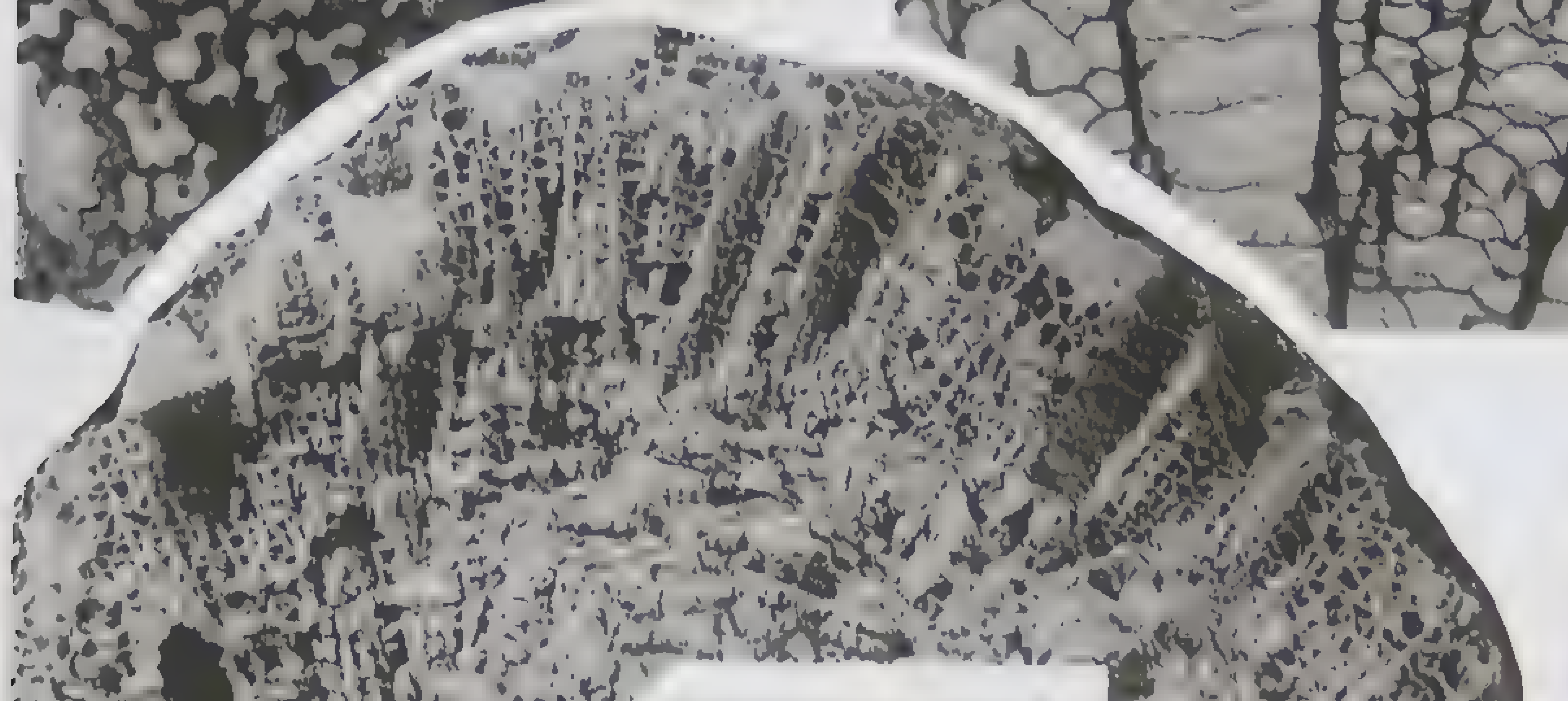

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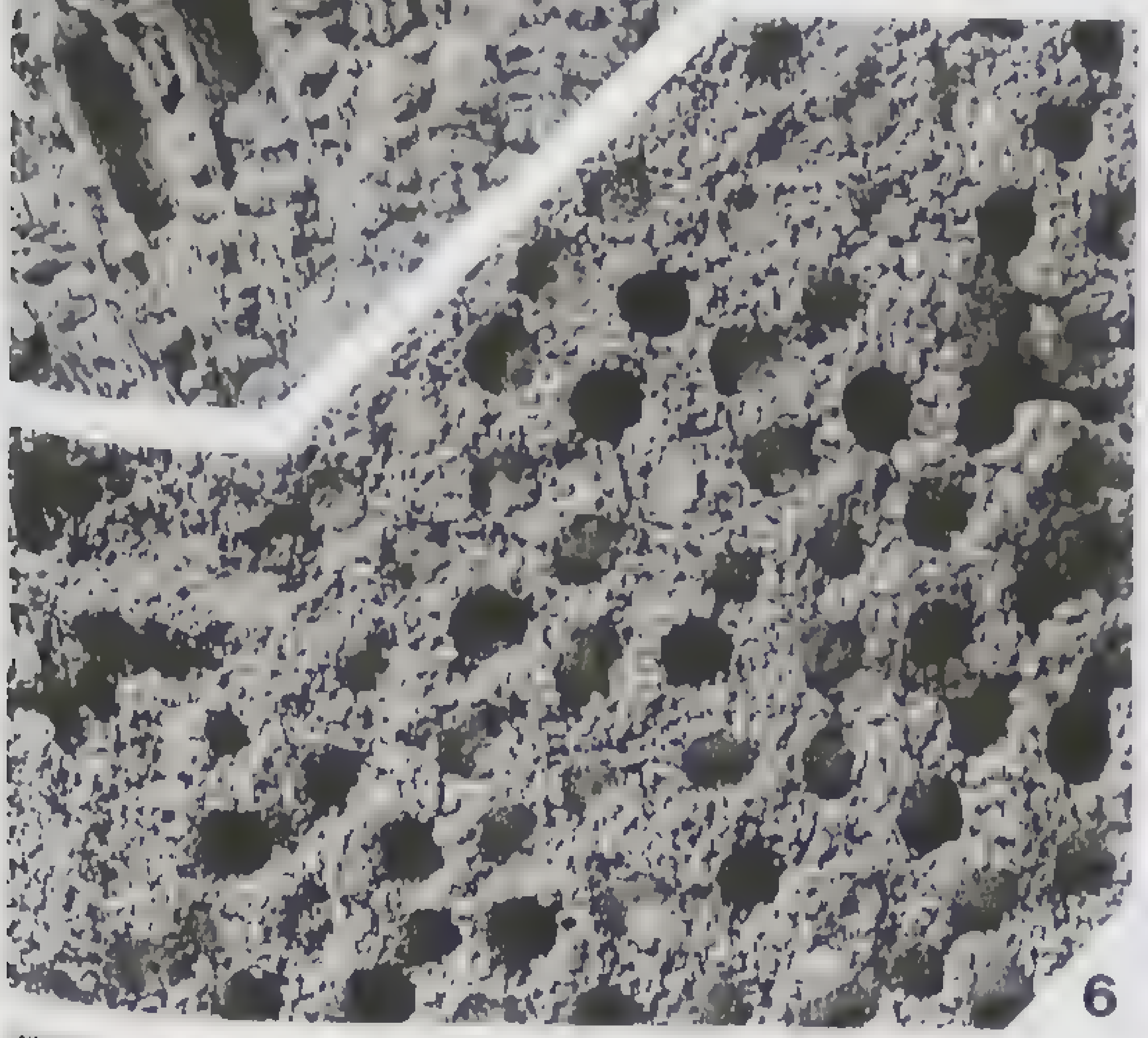

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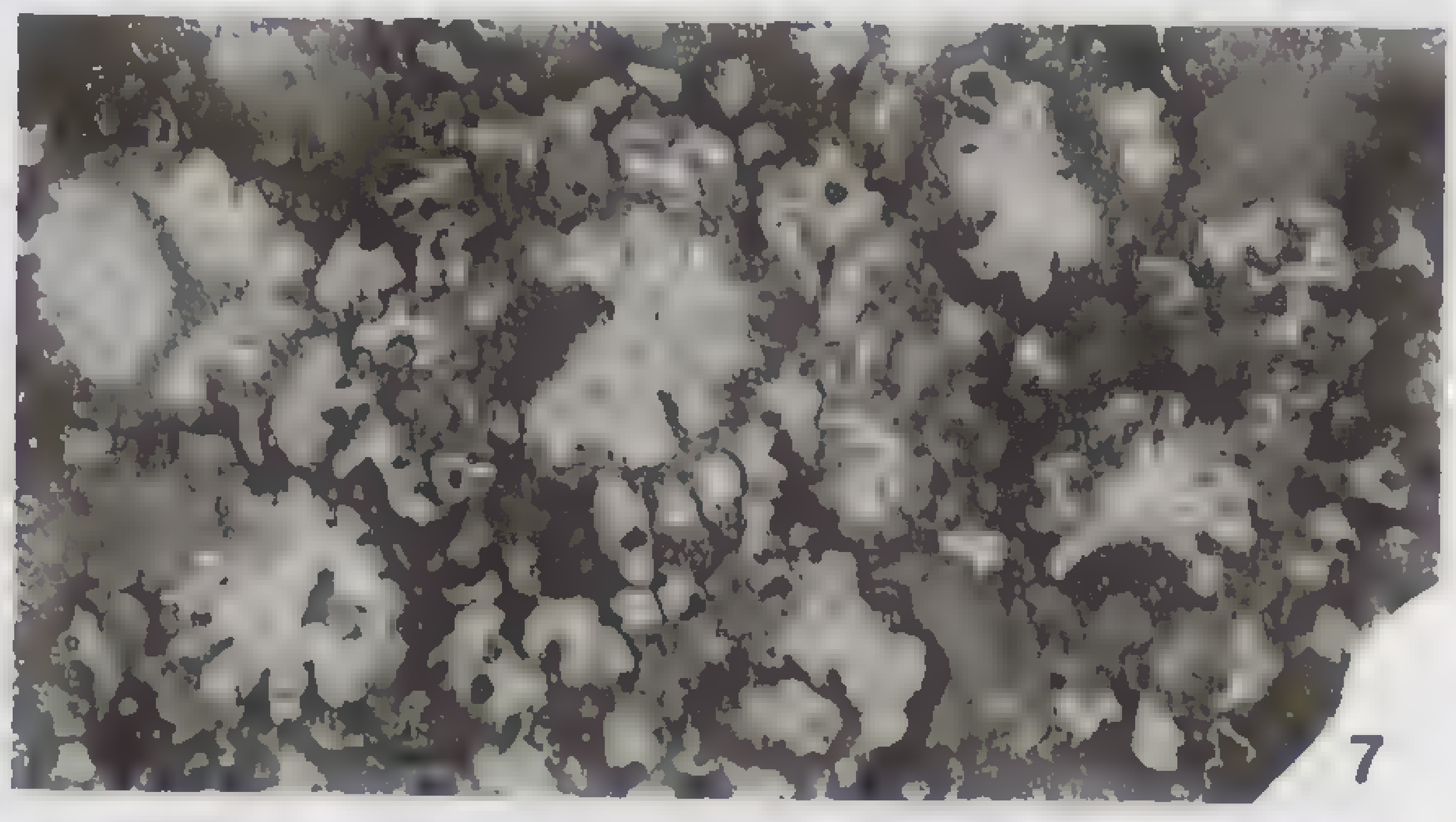

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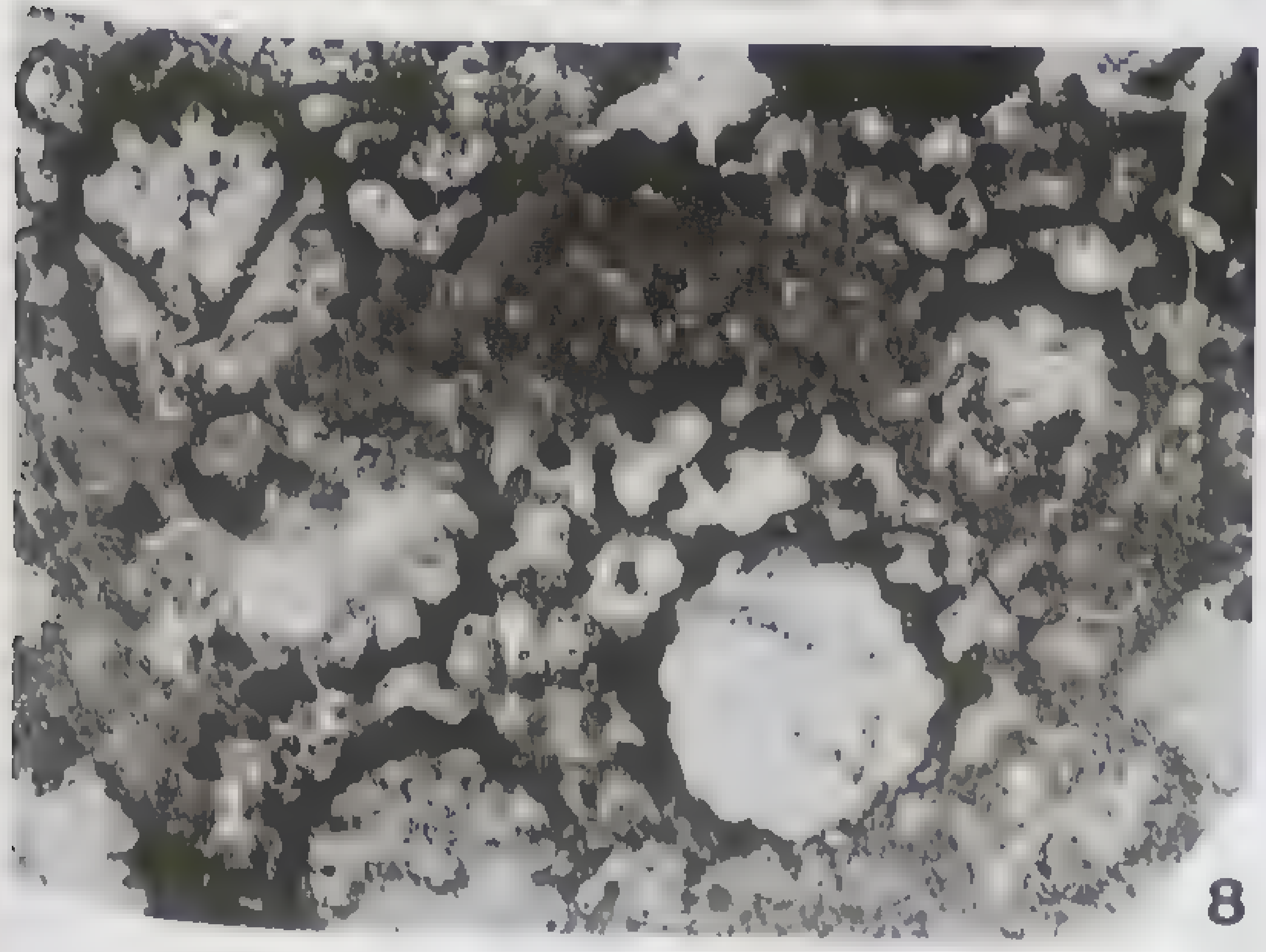

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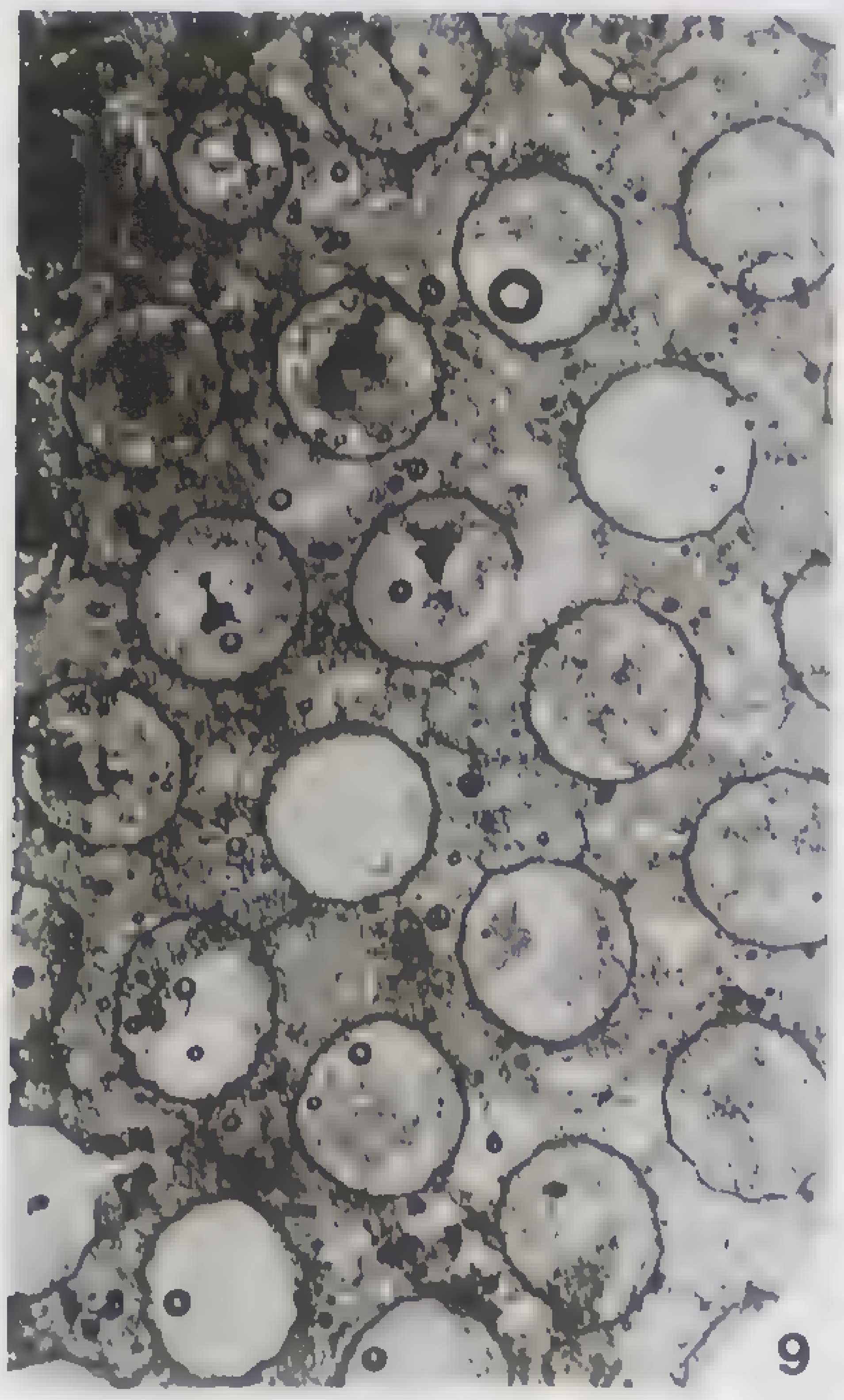

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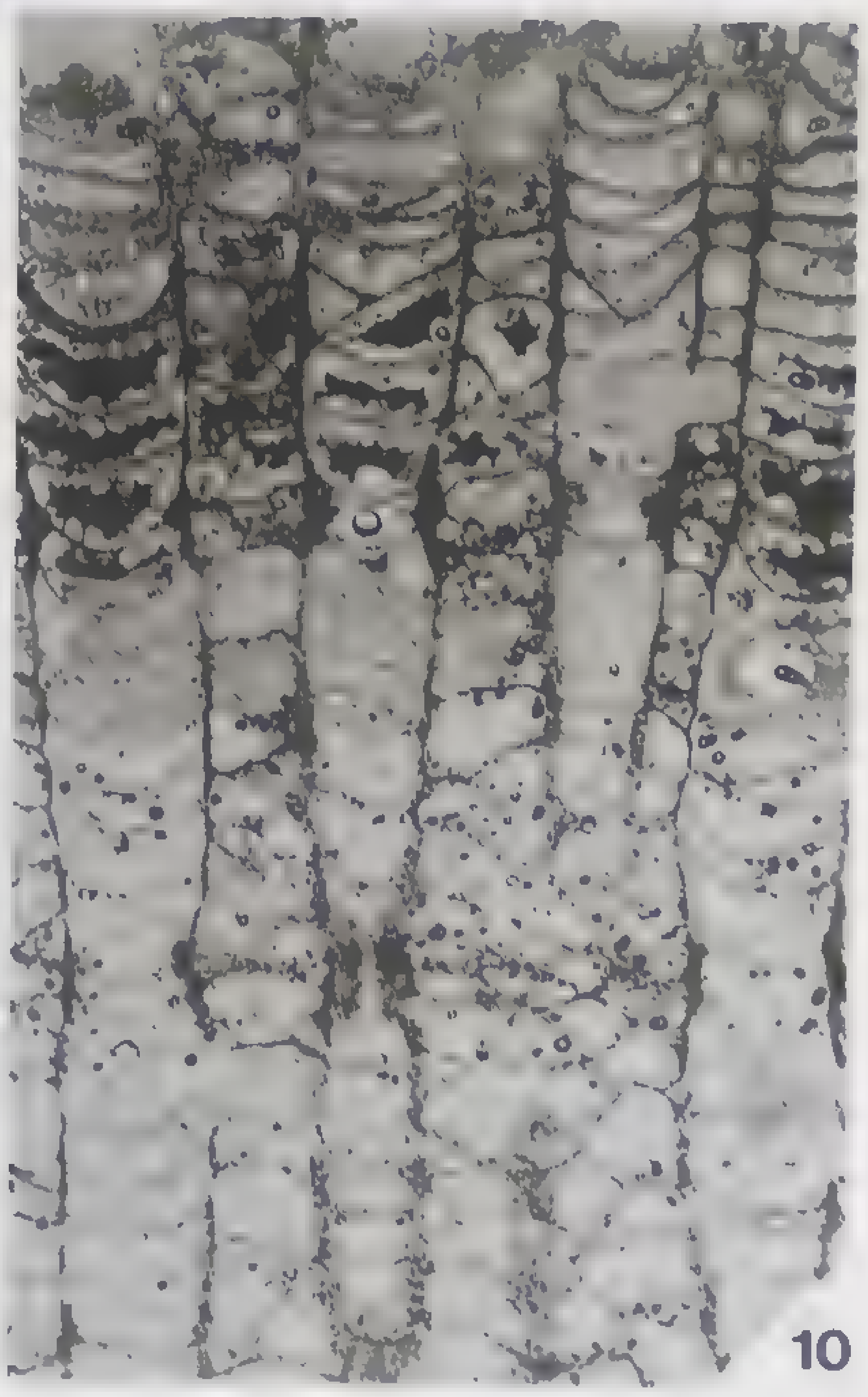

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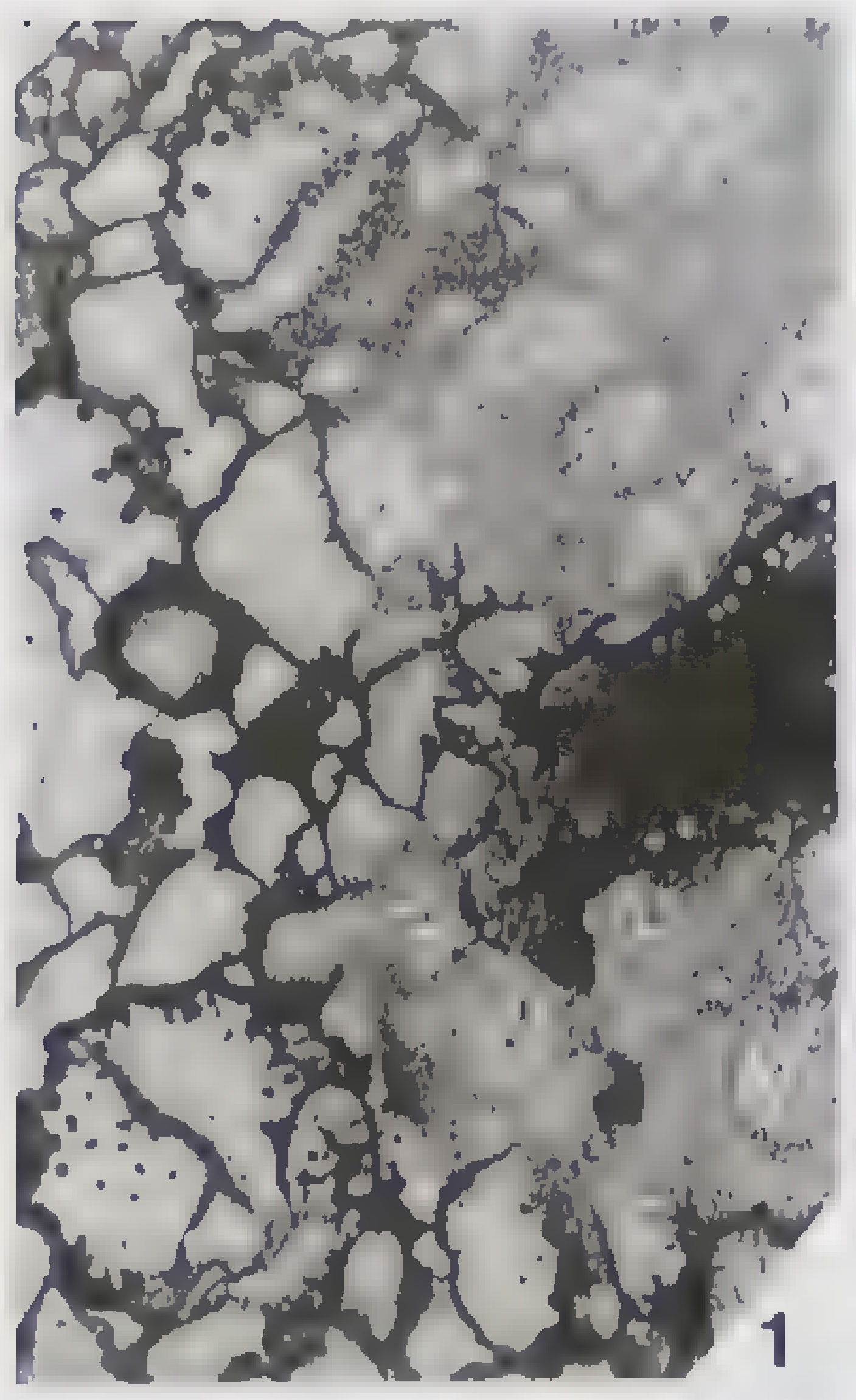
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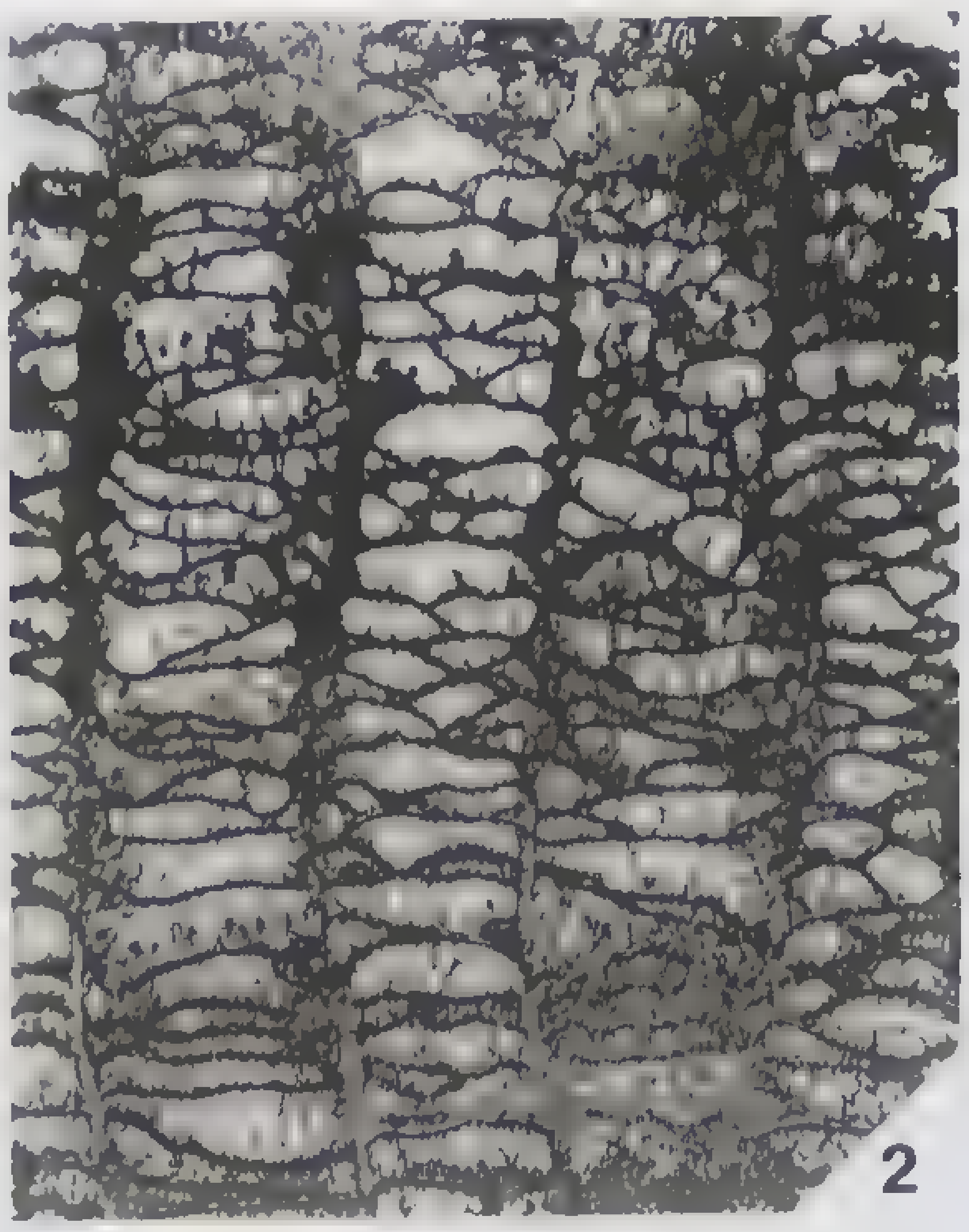
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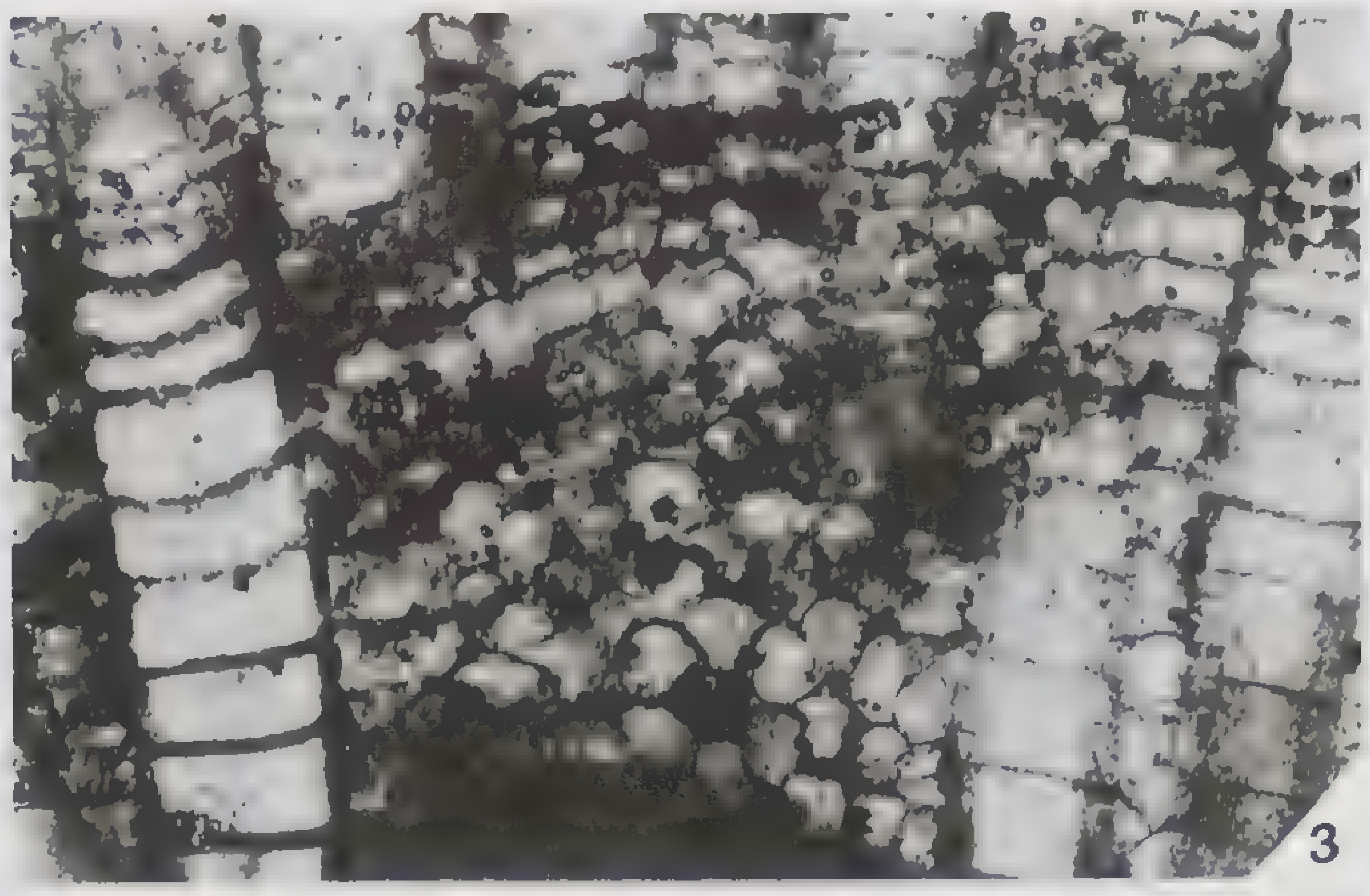
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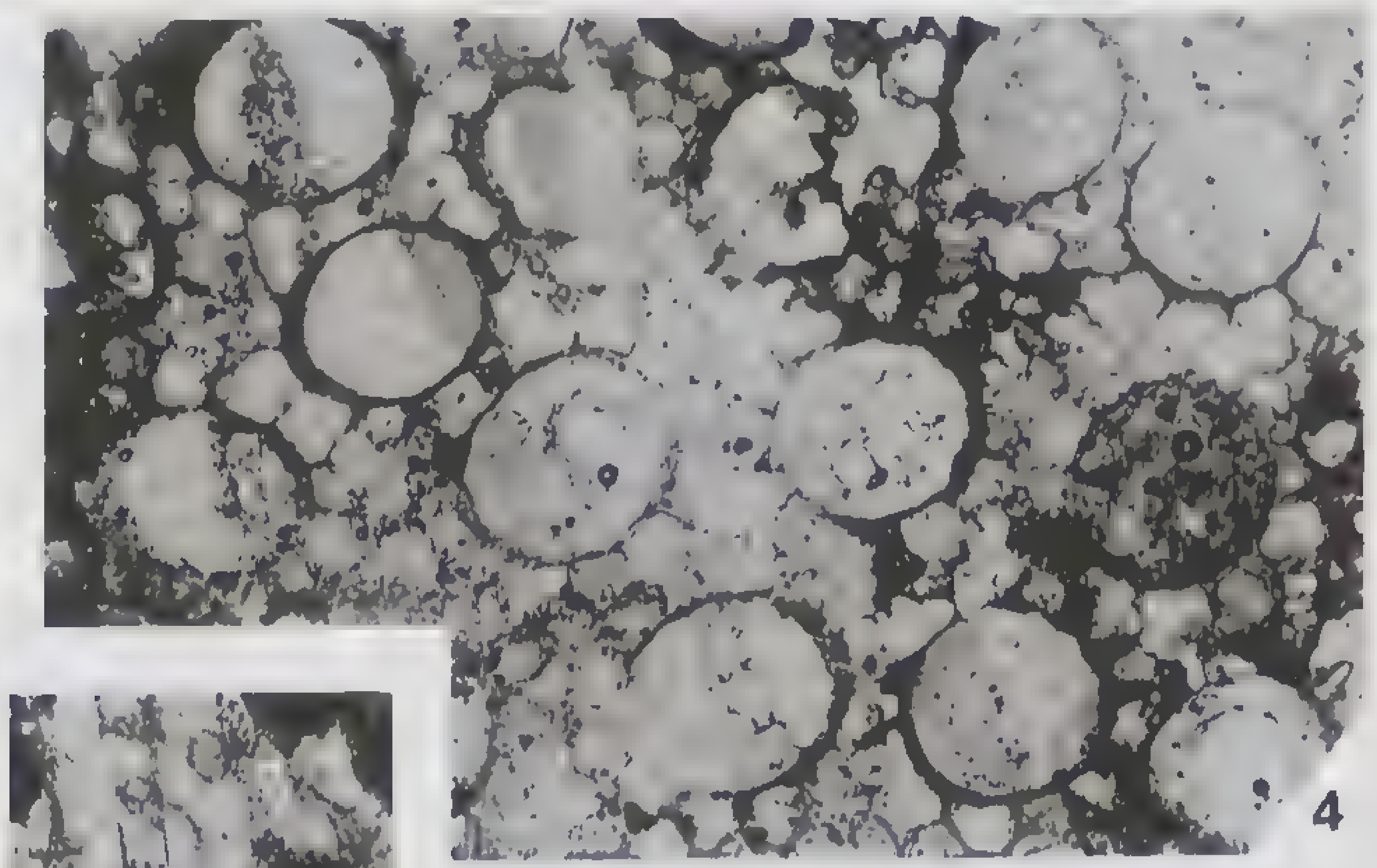
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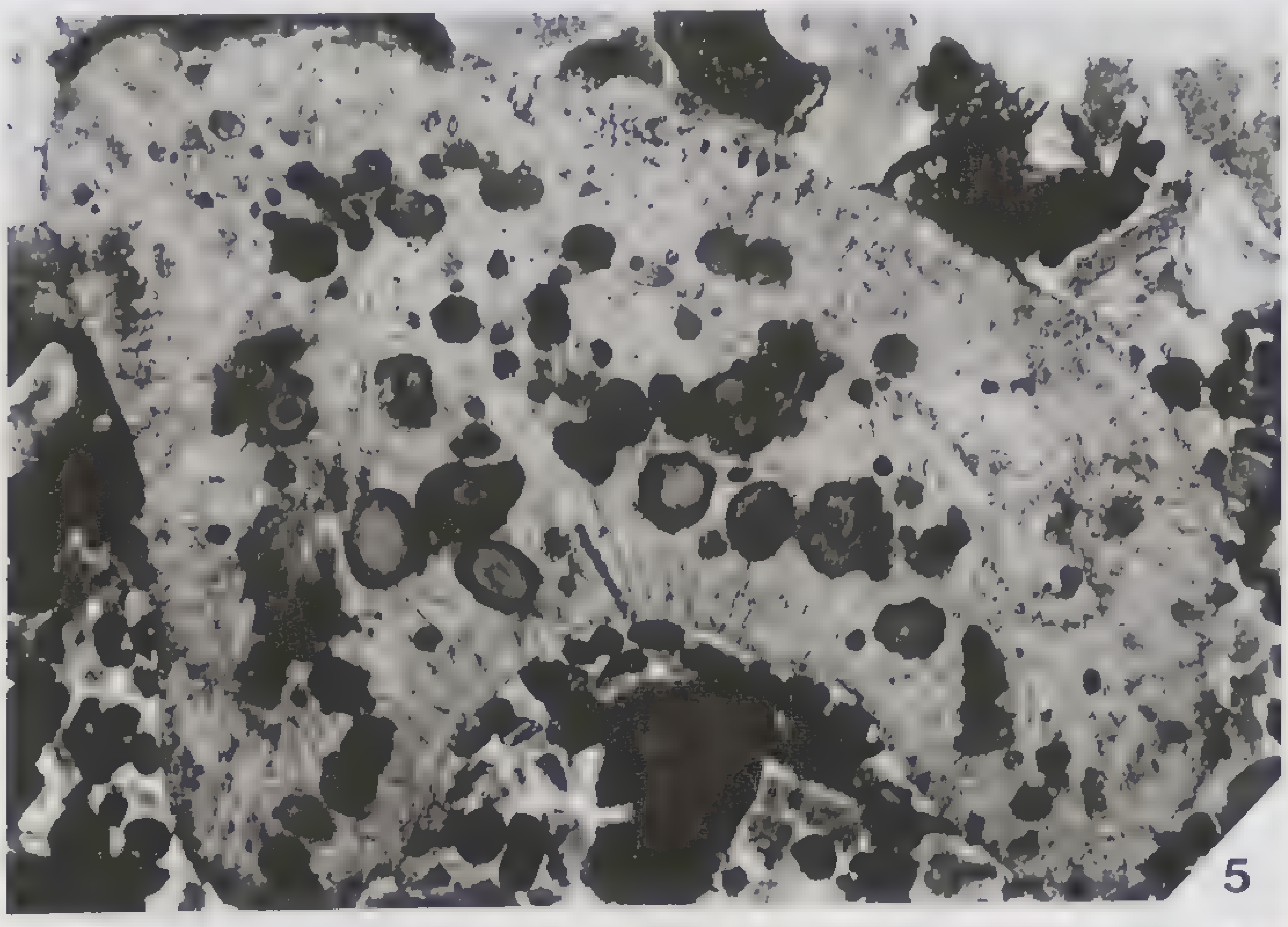
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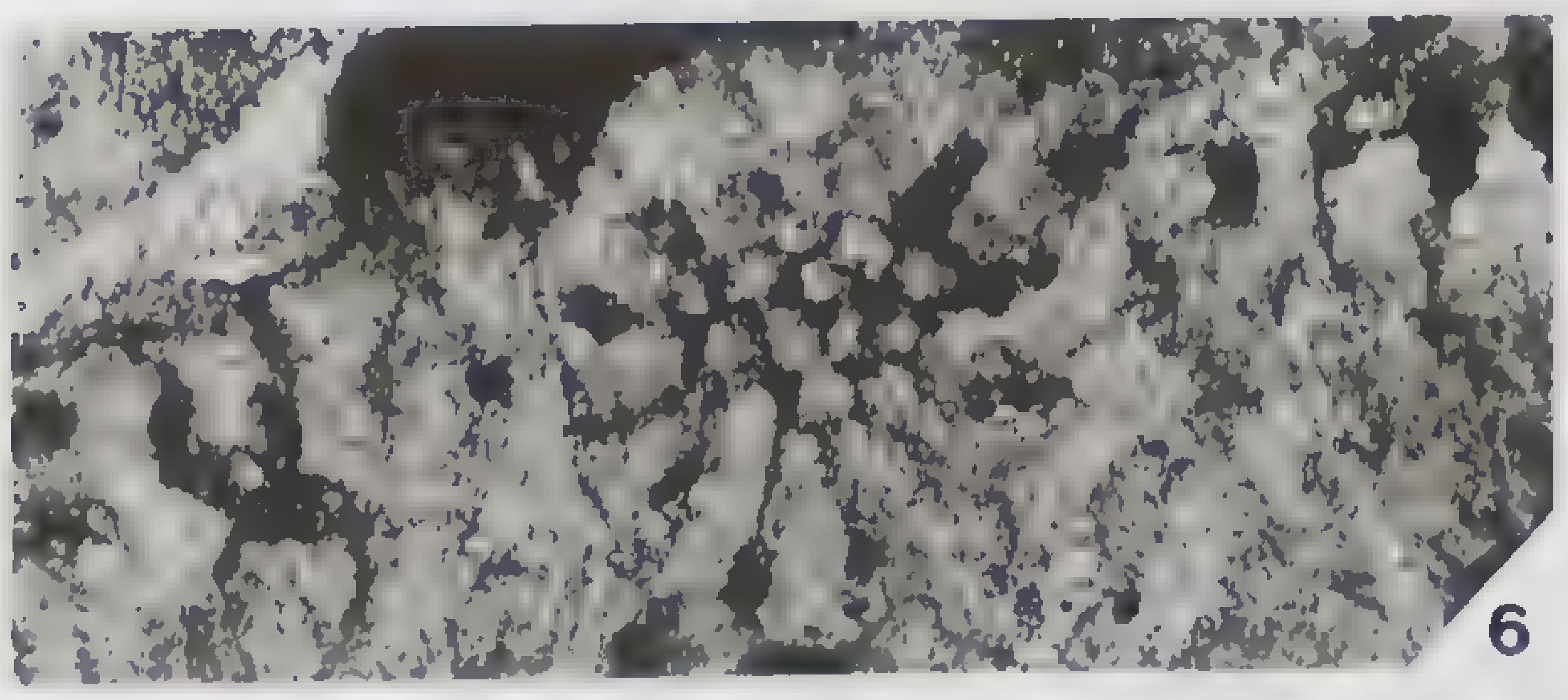
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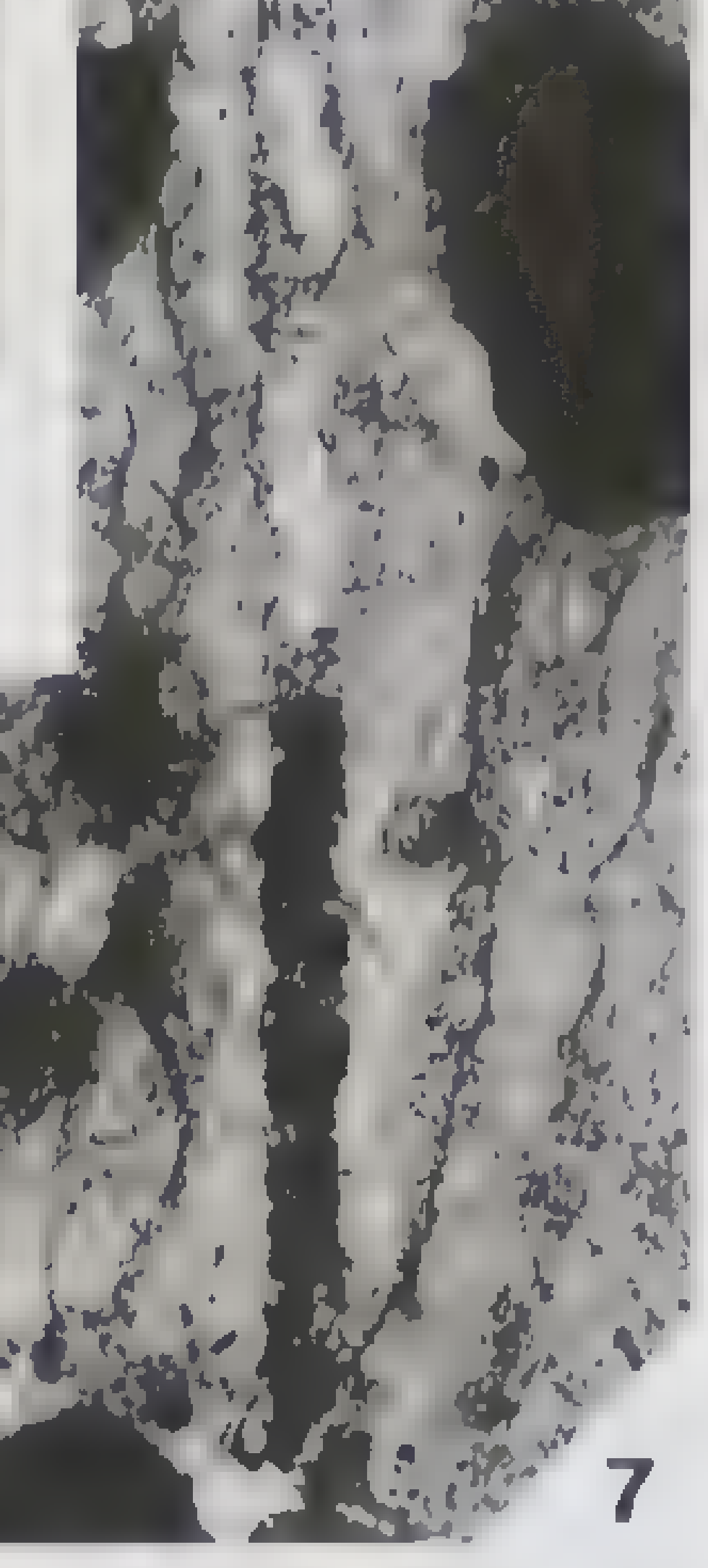
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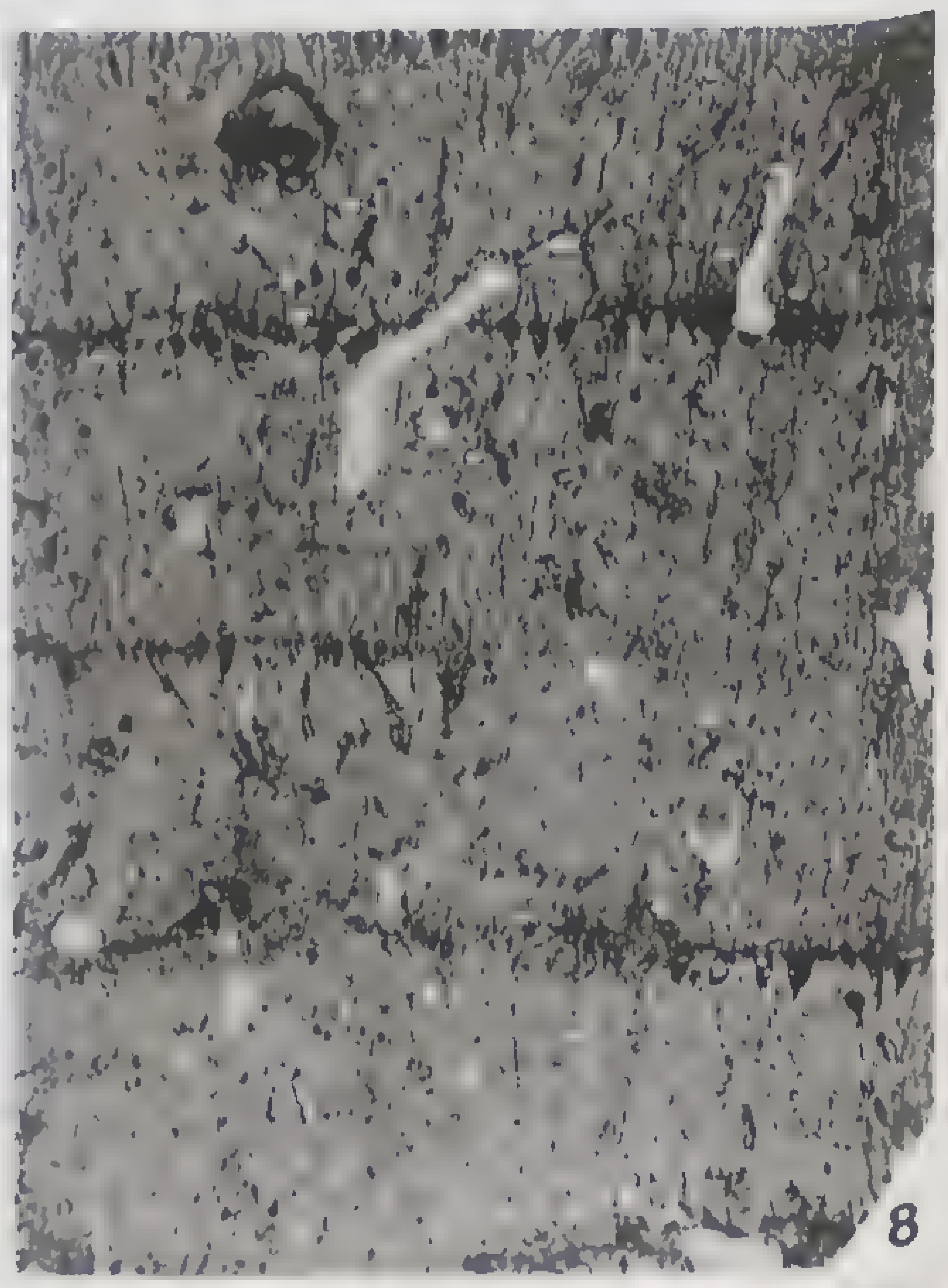
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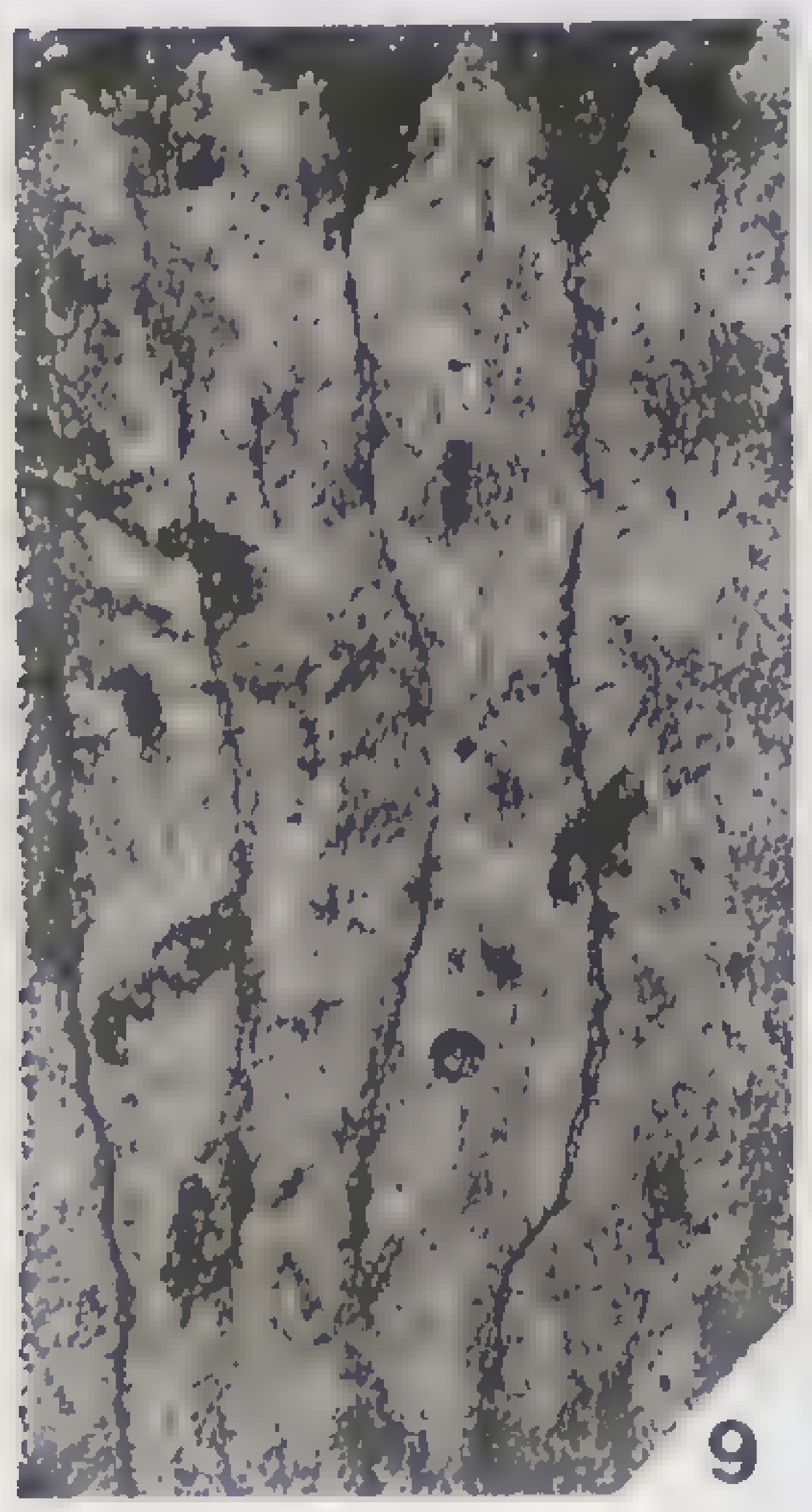
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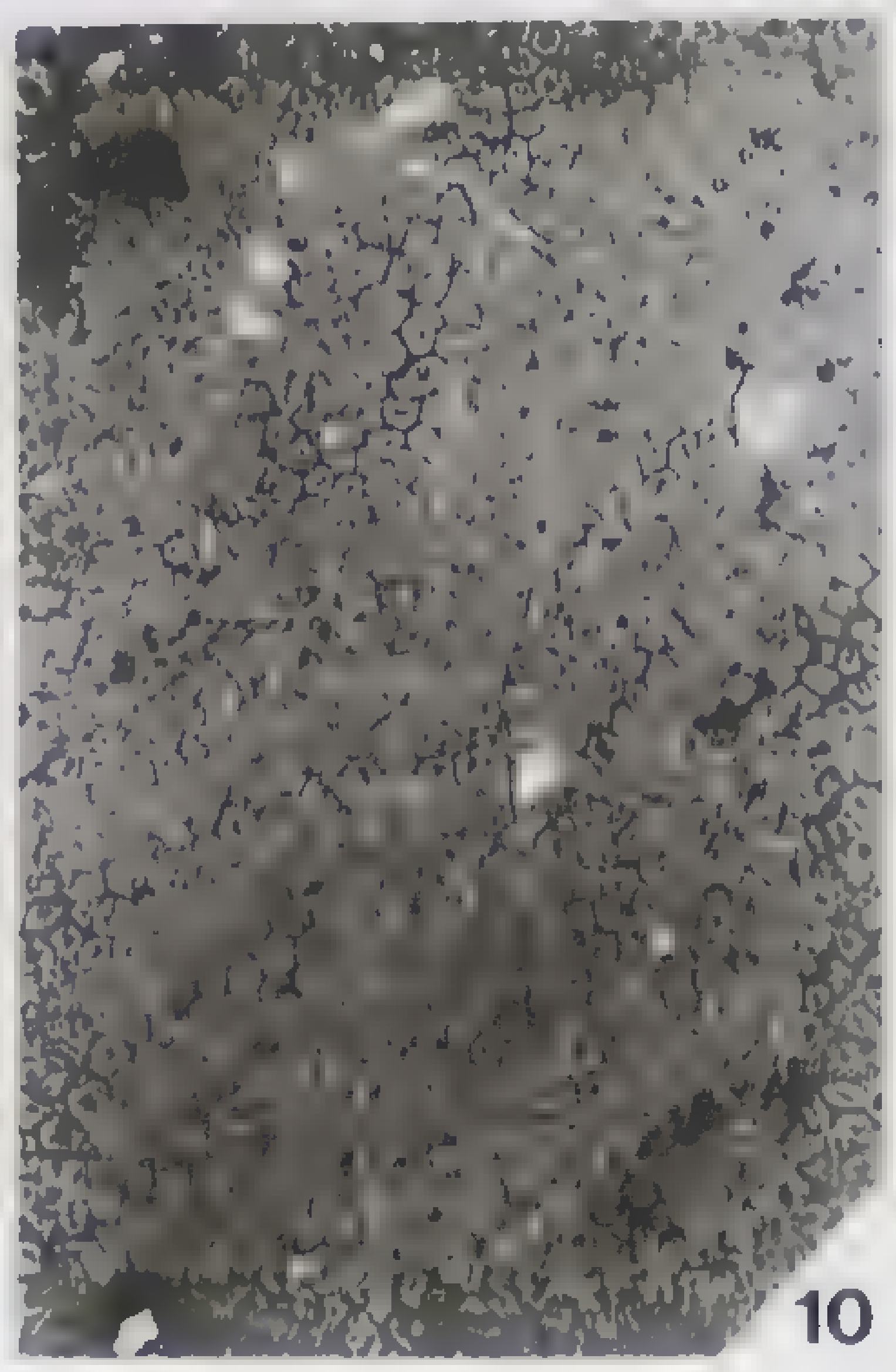
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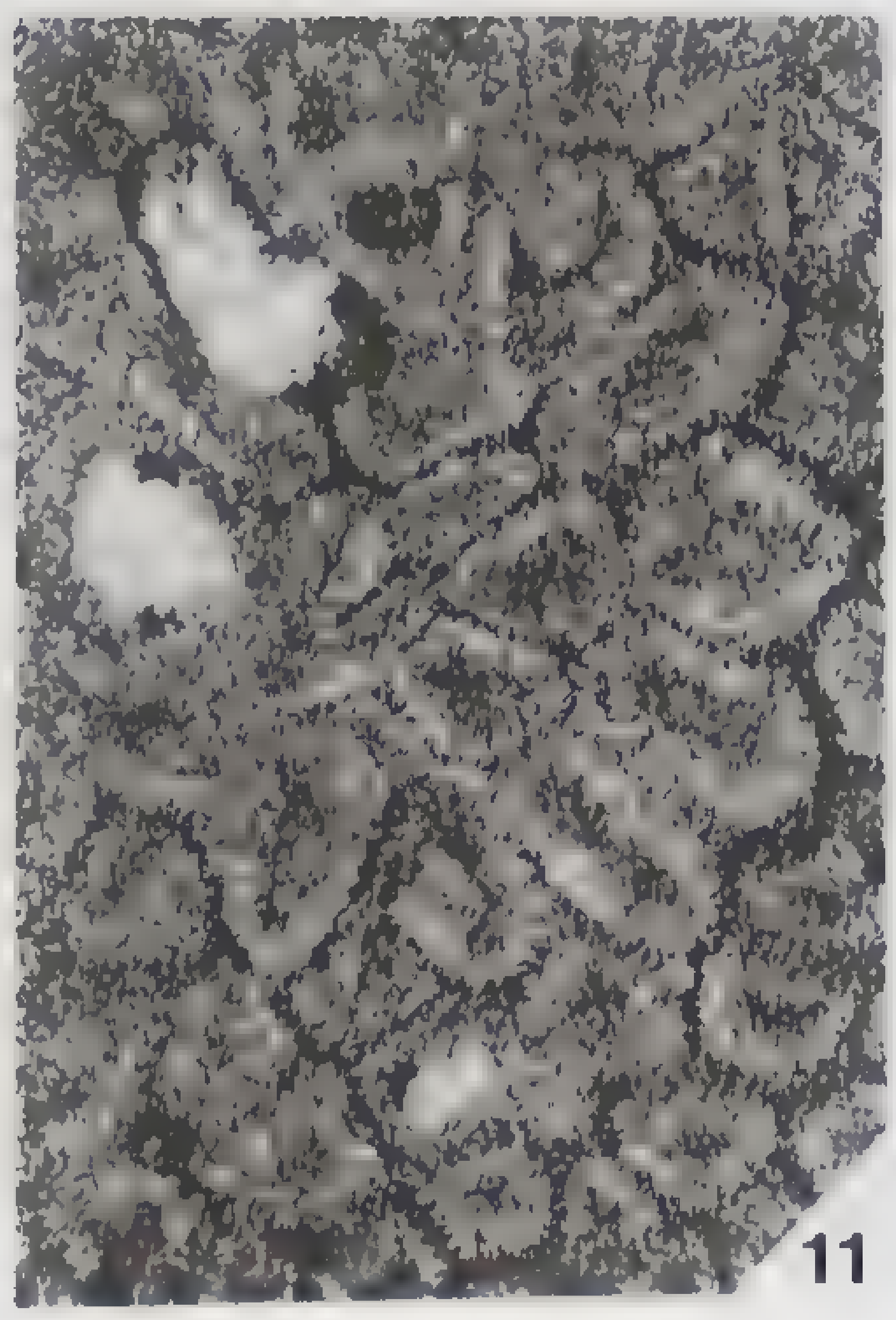
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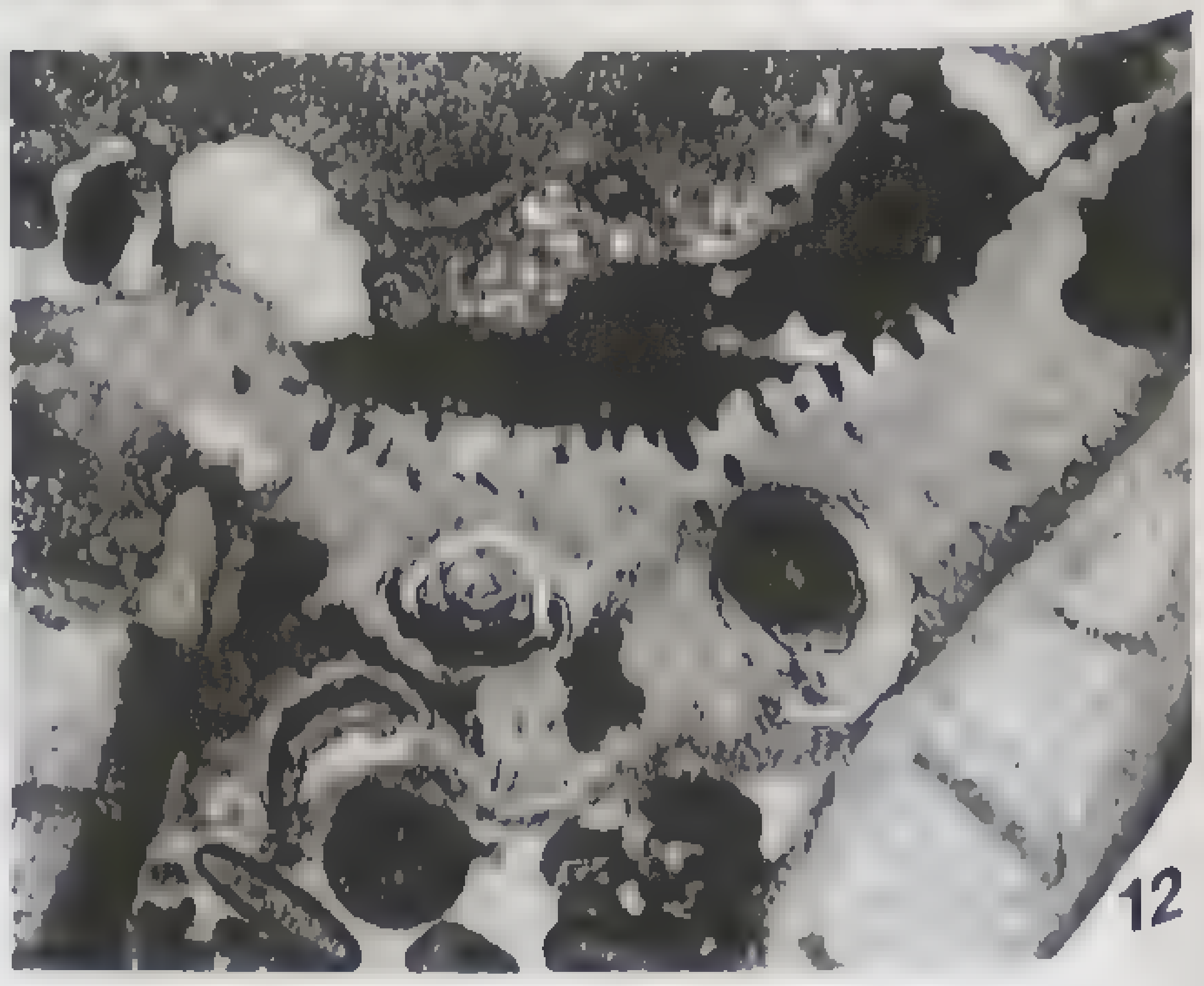
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EXPLANATION OF PLATE 8

Figure Page

1, 2. ***Propora*** species A 63

[1, 2, Sexton Creek Limestone, near Thebes, Illinois.]

1, 2. UI C-1403: 1, transverse section, ×5; 2, longitudinal section, ×5.

3, 4. ***Plasmopora*** species cf. ***P. logani*** Young and Noble, 1990b 64

[3, 4, Cyrene Formation, near Edgewood, Missouri.]

3, 4. UI C-865b: 3, longitudinal section, ×8; 4, transverse section, ×8.

5–7. ***Acidolites*** species A 65

[5–7, Leemon Formation, Section 31 (Thebes North).]

5–7. UI C-889b: 5, section through entire corallum (includes longitudinal and transverse sections of corallites), ×10; 6, transverse section showing a single tabularium (detail from top center of corallum in 5, turned 30° counterclockwise), ×40; 7, longitudinal section (detail from bottom center of corallum in 5), ×40.

8–12. ***Protaraea*** species A 66

[8–12, *Brevilamnulella* beds, Keel Formation, Section-interval 23-2 (Lawrence Quarry) (8–11, site 23i; 12, site 23iv).]

8–11. USNM 485778: 8, longitudinal section (dark horizontal layers are sediment inclusions), ×8; 9, longitudinal section, ×40; 10, transverse section, ×8; 11, transverse section showing a single tabularium (detail from upper left of center in 10), ×40; note microborings in 8–11 (micrite-filled microborings are darker than corallum, cement-filled microborings are lighter).

12. USNM 485780c: longitudinal section showing corallum (center) encrusting corallites of *Halysites alexandricus* (lower left, lower right), ×12.

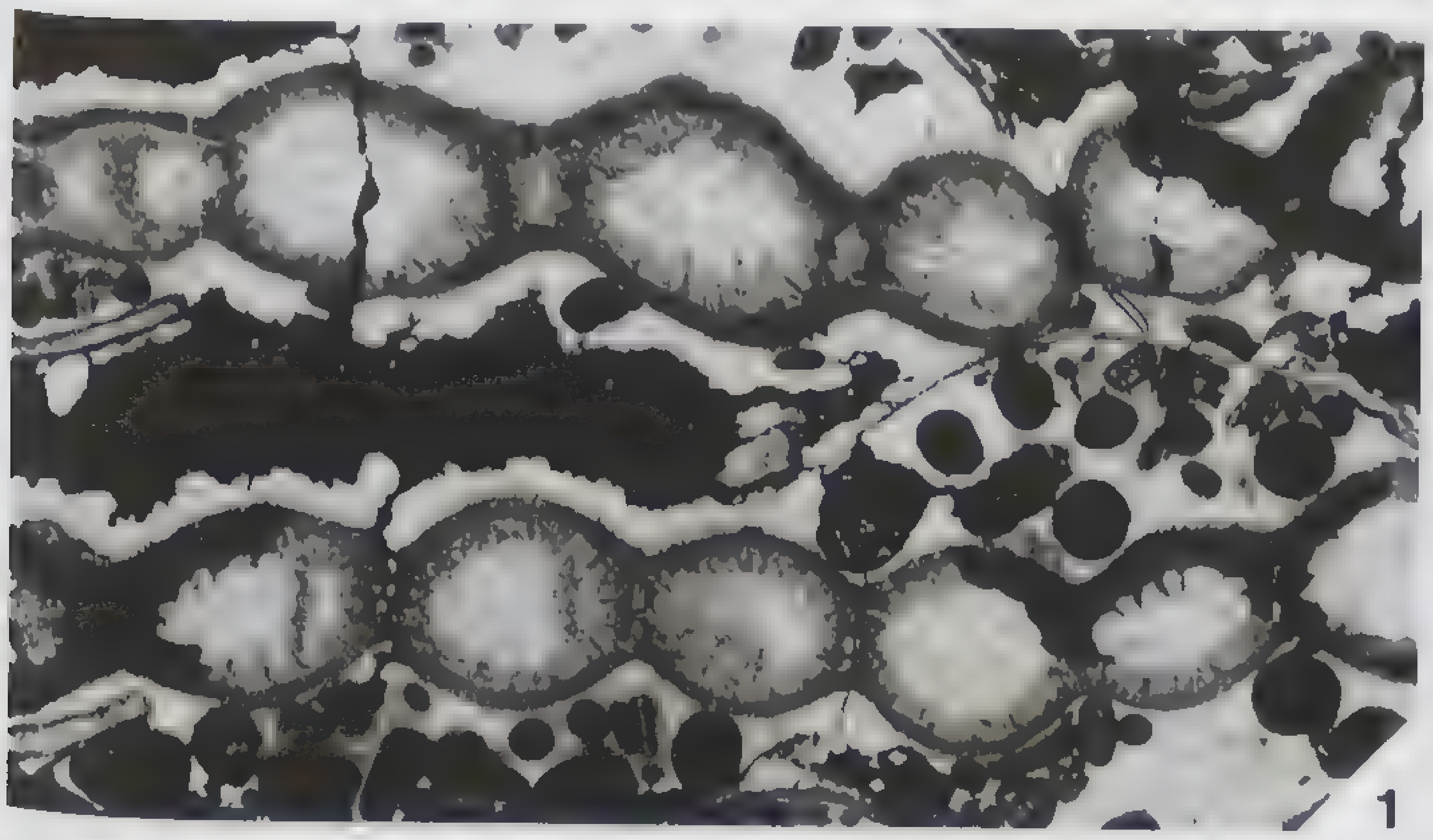
EXPLANATION OF PLATE 9

Figure Page

1–11. ***Halysites alexandricus,*** new species 67

[1–8, *Brevilamnulella* beds, Keel Formation, Section-interval 23-2 (Lawrence Quarry) (1–3, site 23i; 4–6, site 23ii; 7, site 23iv; 8, site 23iii); 9–11, Keel Formation (undivided), Section-interval 23a-1 (Lawrence Quarry).]

- 1–3. USNM 485782 (paratype): 1, transverse section, ×8; 2, transverse section, ×20; 3, transverse section showing wall structure, ×40.
- 4–6. USNM 458778 (paratype): 4, transverse section, ×8; 5, longitudinal section, ×8; 6, longitudinal section showing structure of walls and tubule (detail from lower right of center in 5, turned 10° counterclockwise), ×40.
- 7. USNM 485785b: longitudinal section showing structure of walls and tabulae, ×40.
- 8. USNM 485779a: longitudinal section through corallum based on a stromatoporoid, ×5.
- 9–11. USNM 423421: 9, transverse section (note corallum of *Keelophyllum oklahomense* attached to ranks), ×8; 10, transverse section showing wall structure (detail from lower right in 9, turned 110° clockwise), ×40; 11, transverse section showing a tubule (detail from right of center in 9, turned 80° clockwise), ×40.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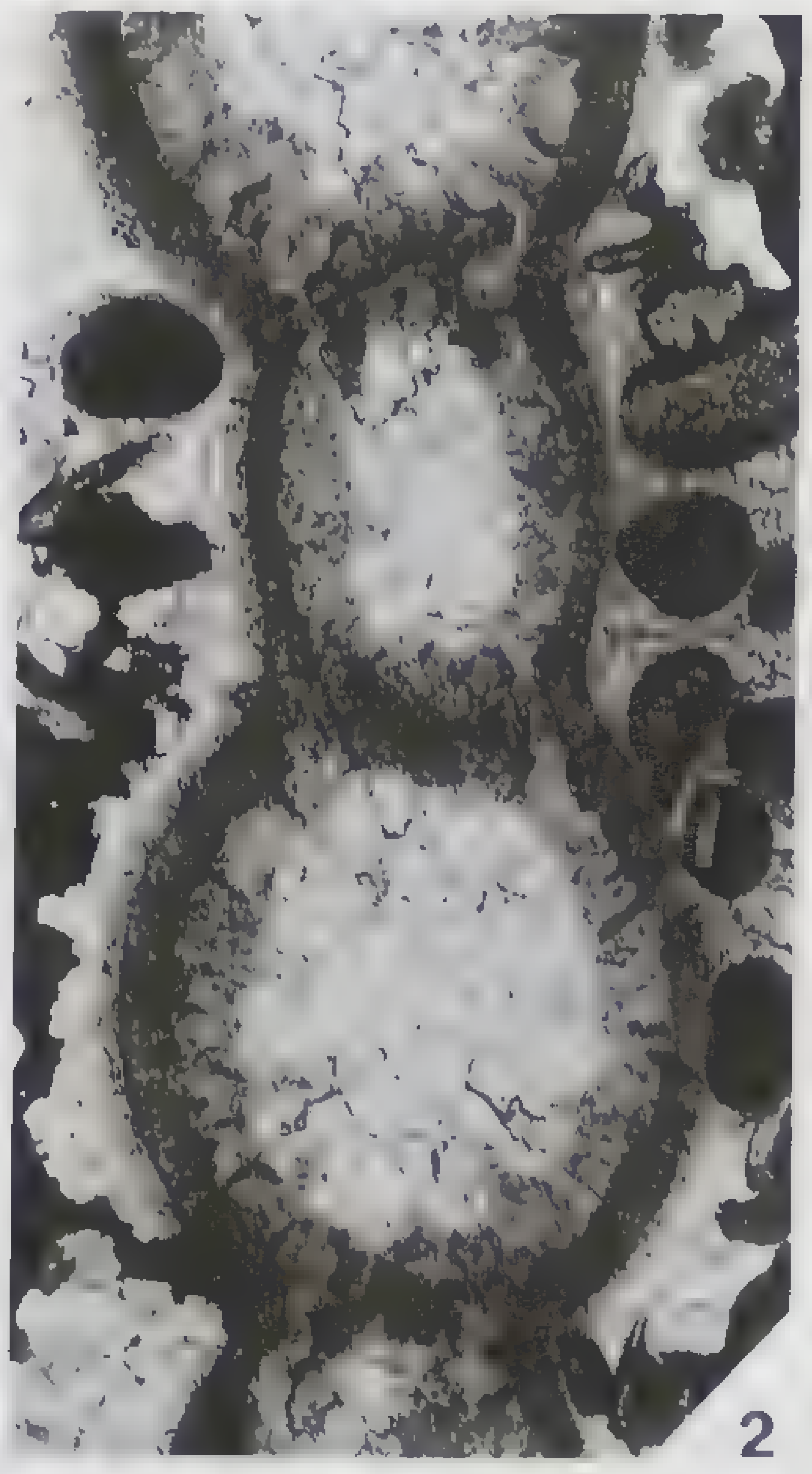
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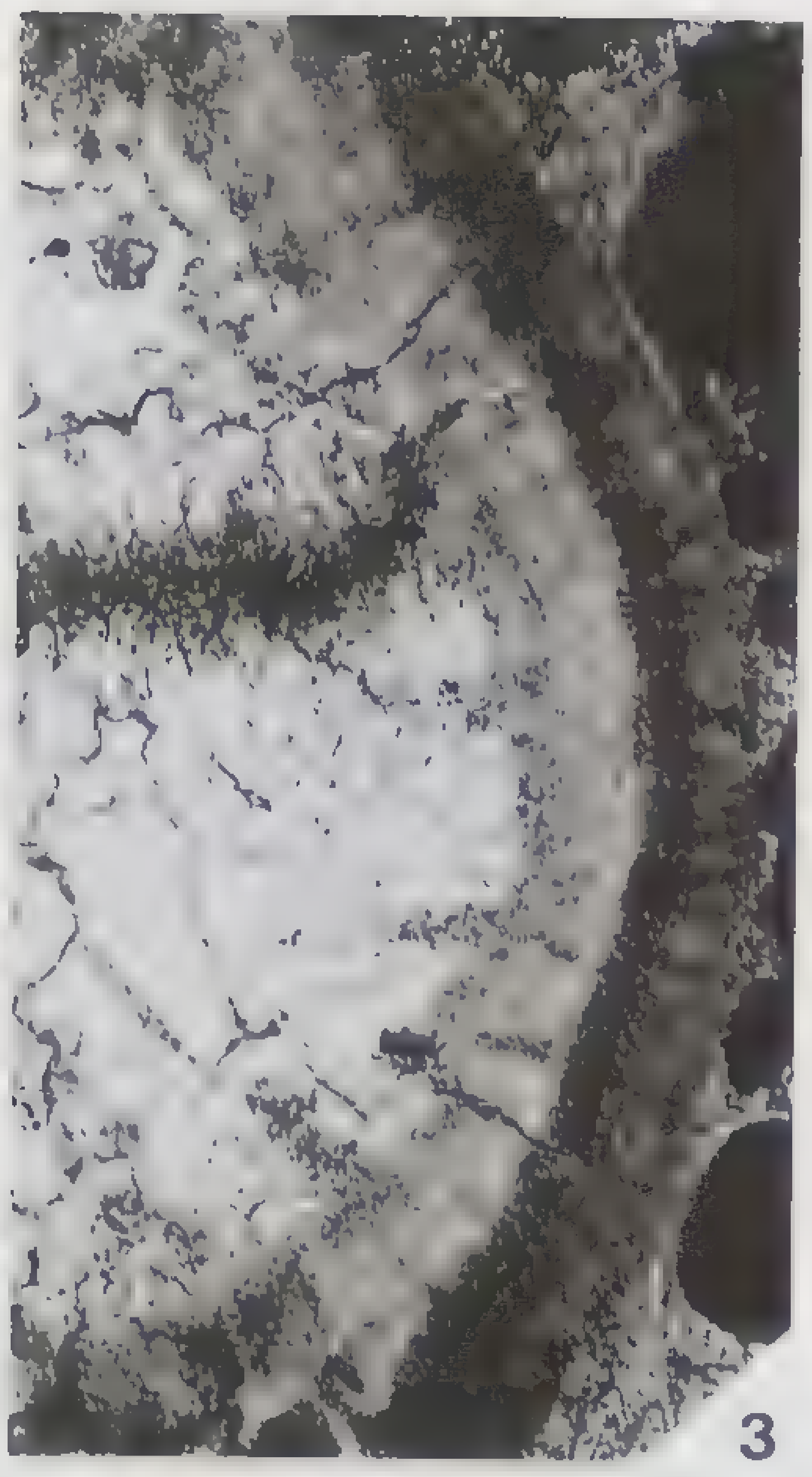
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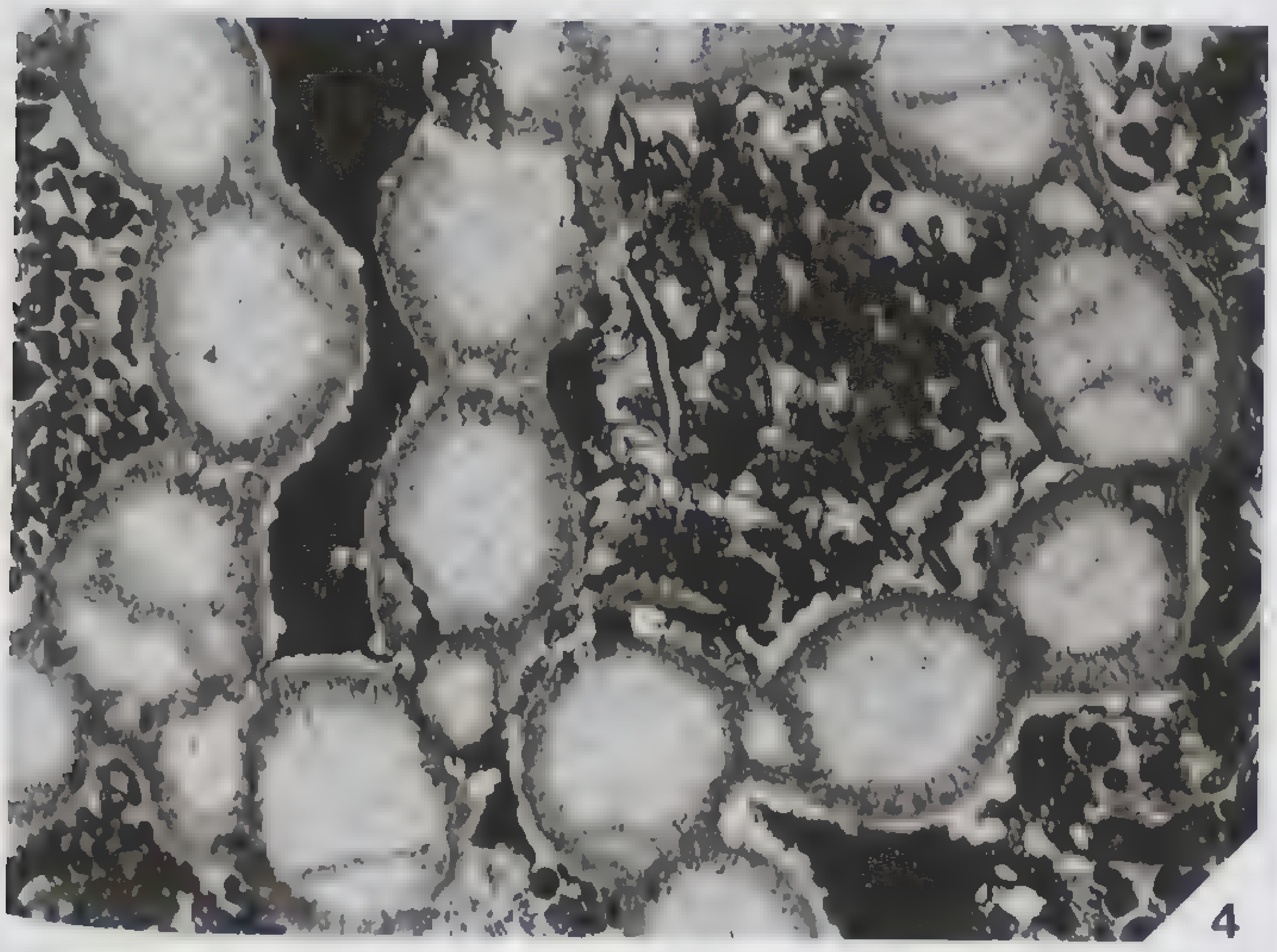
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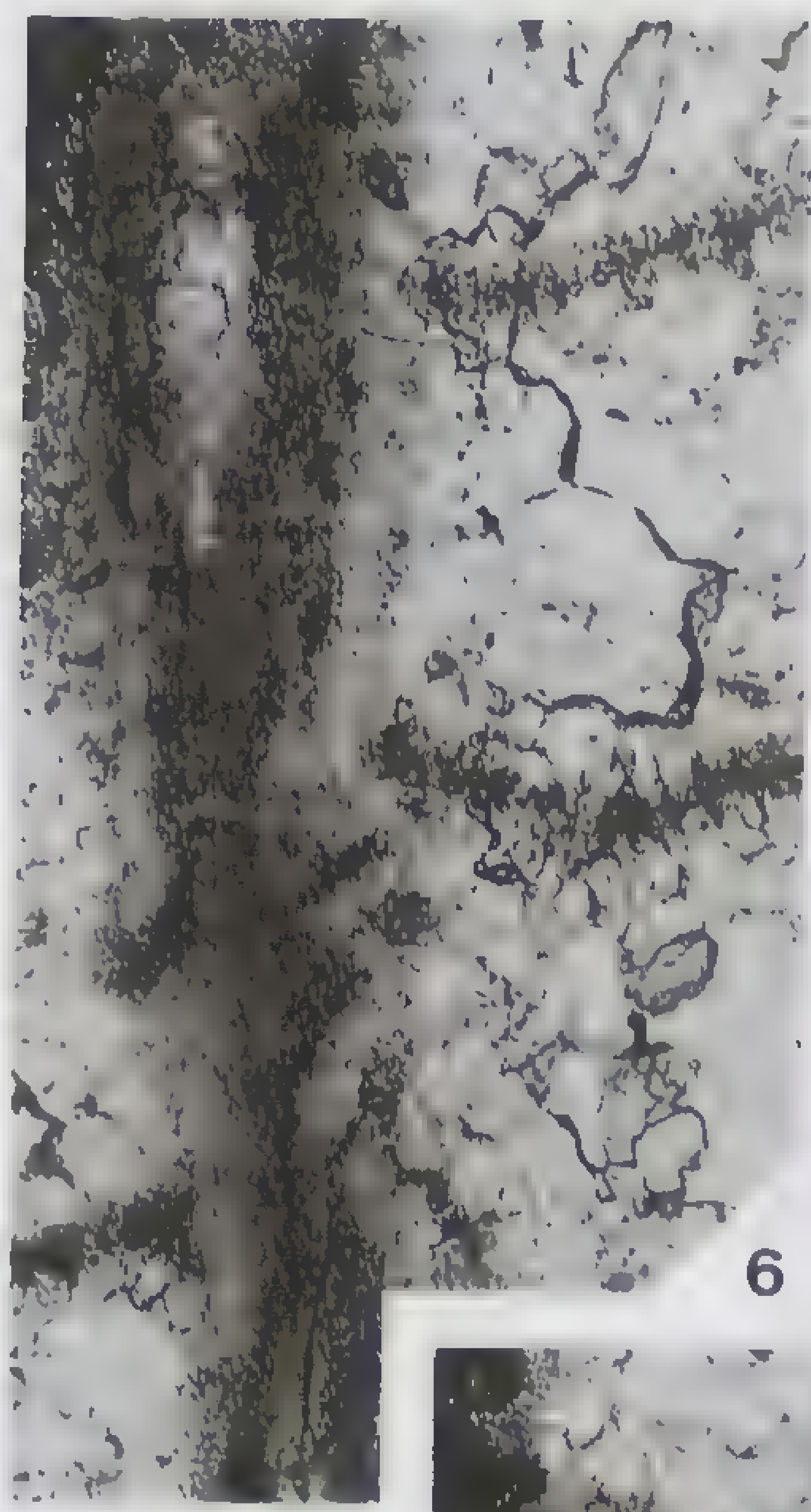
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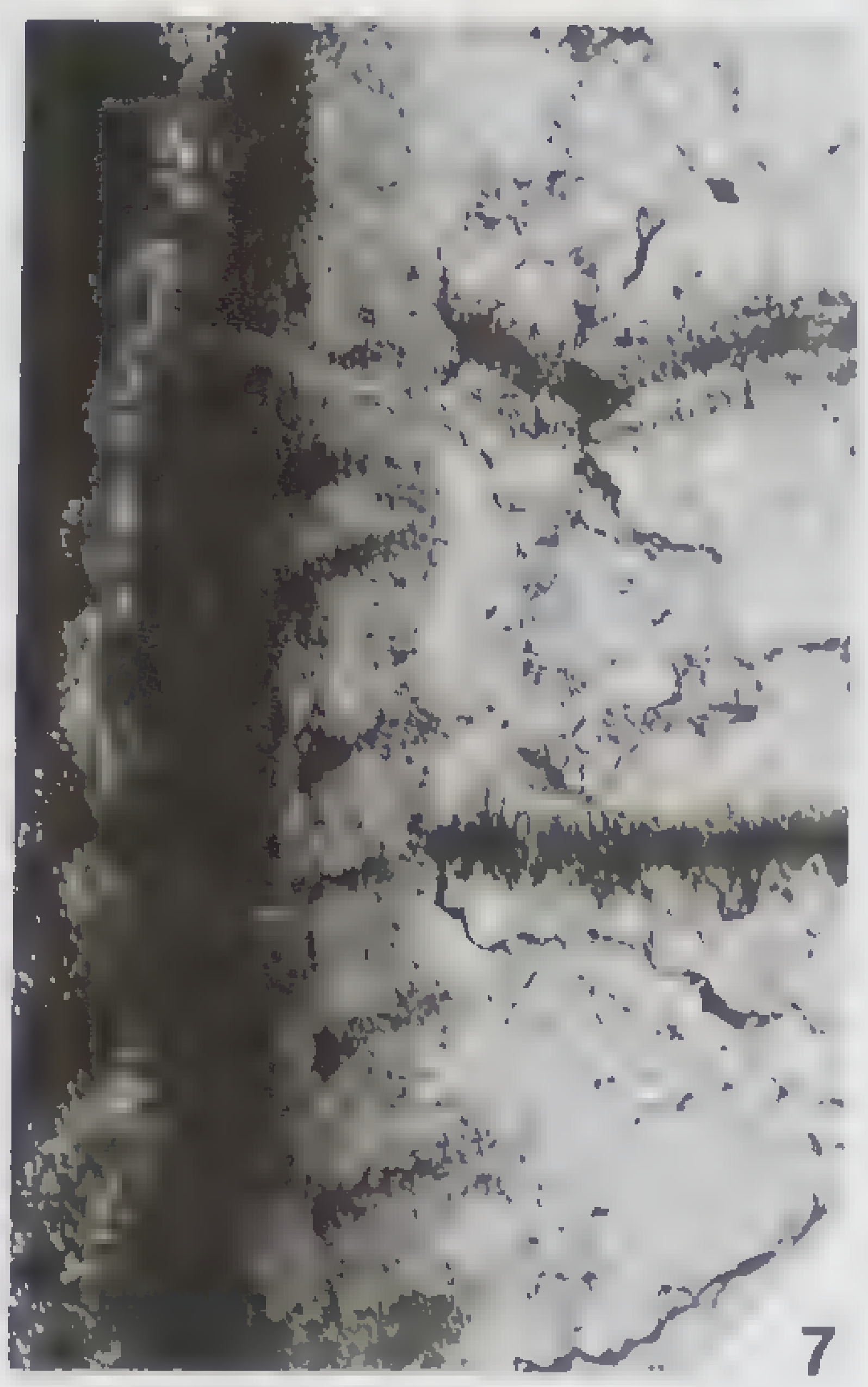
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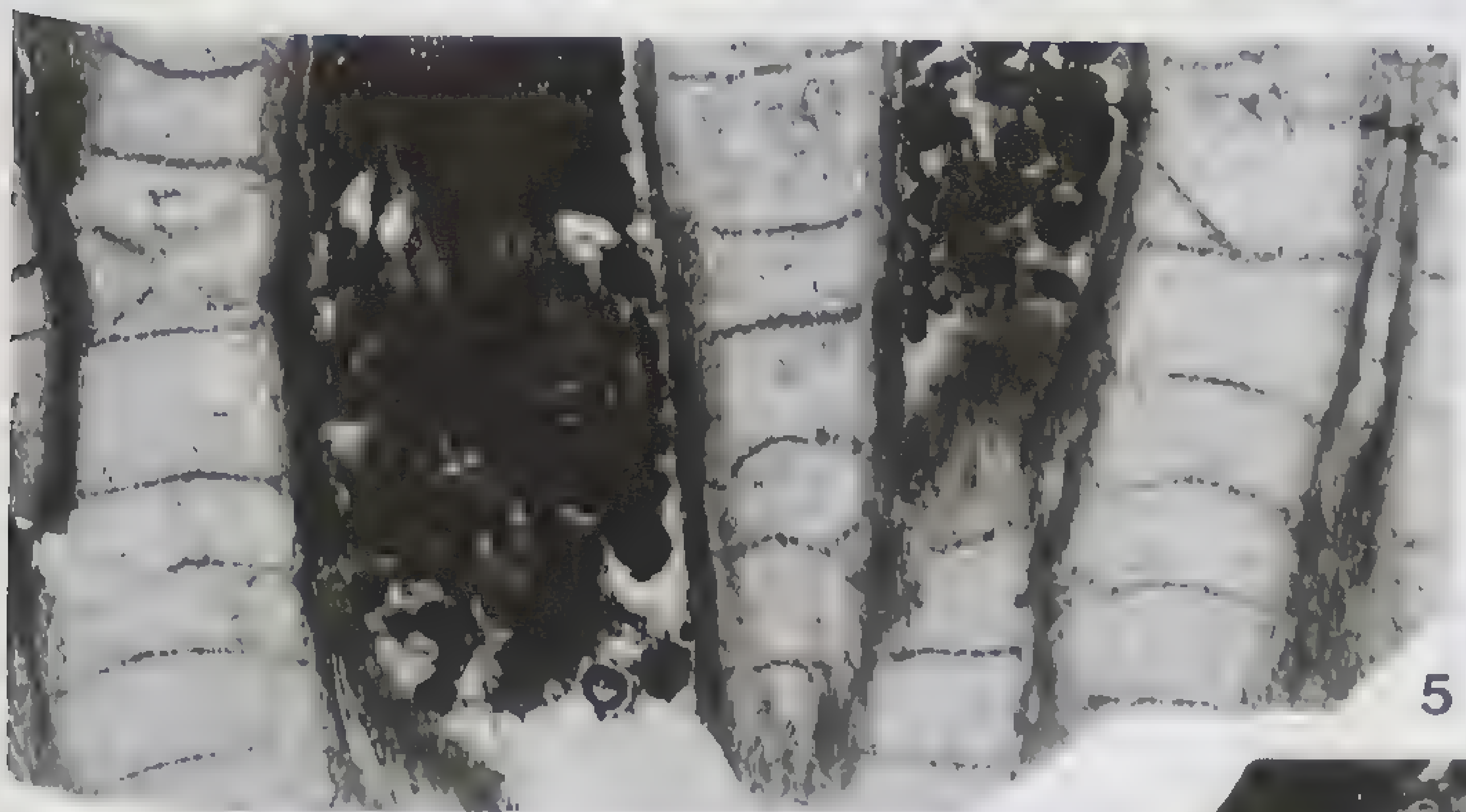
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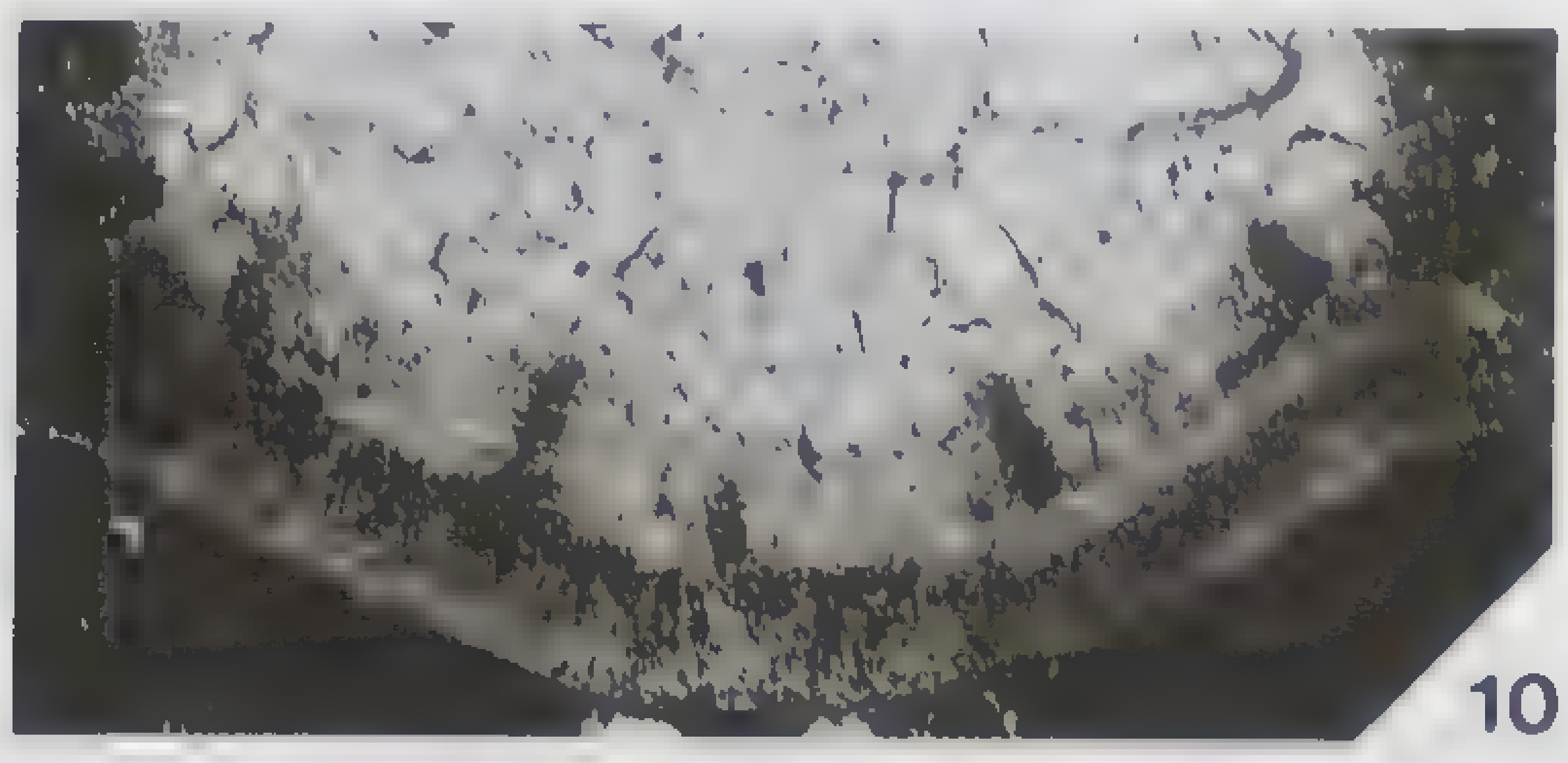
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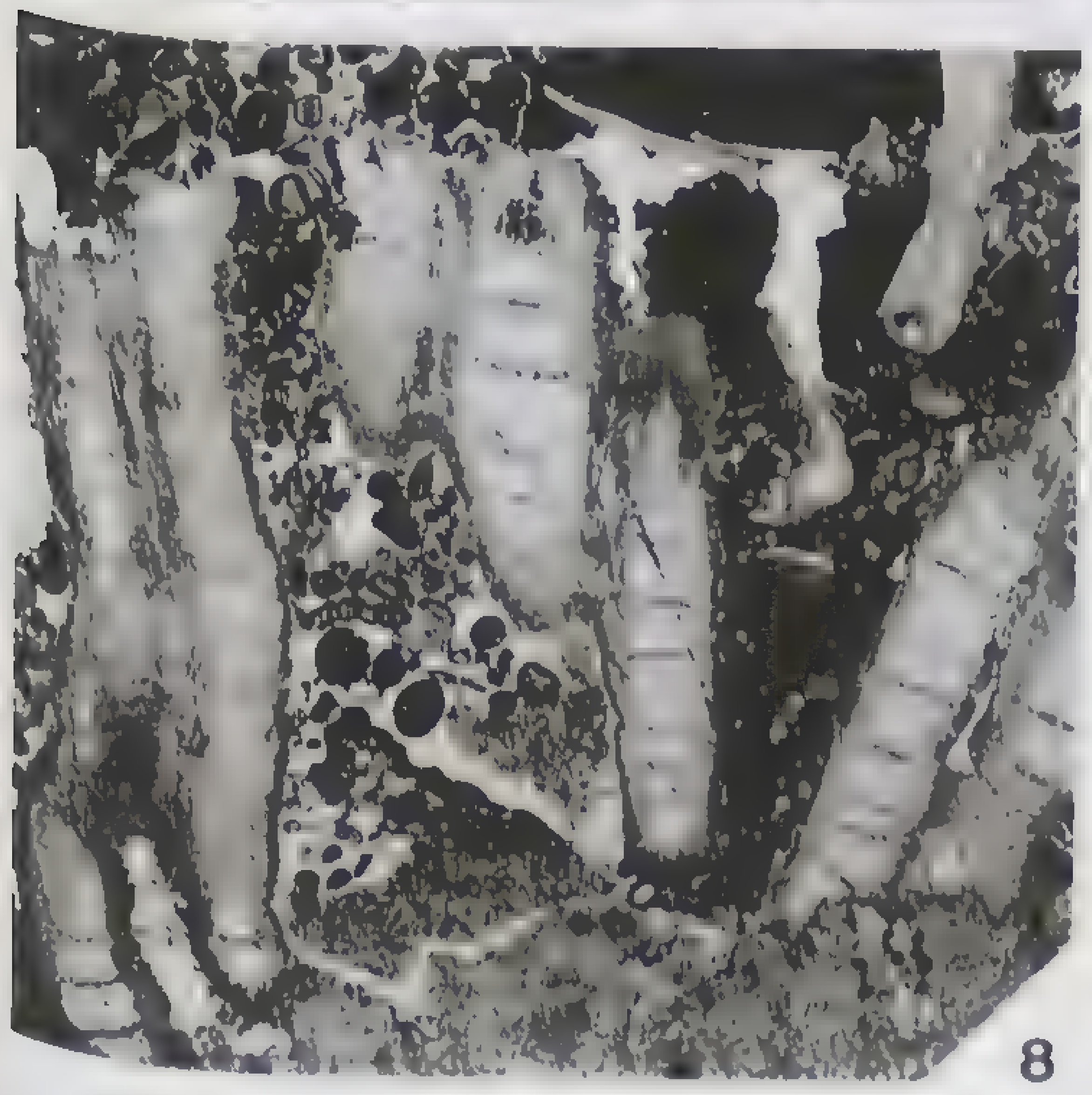
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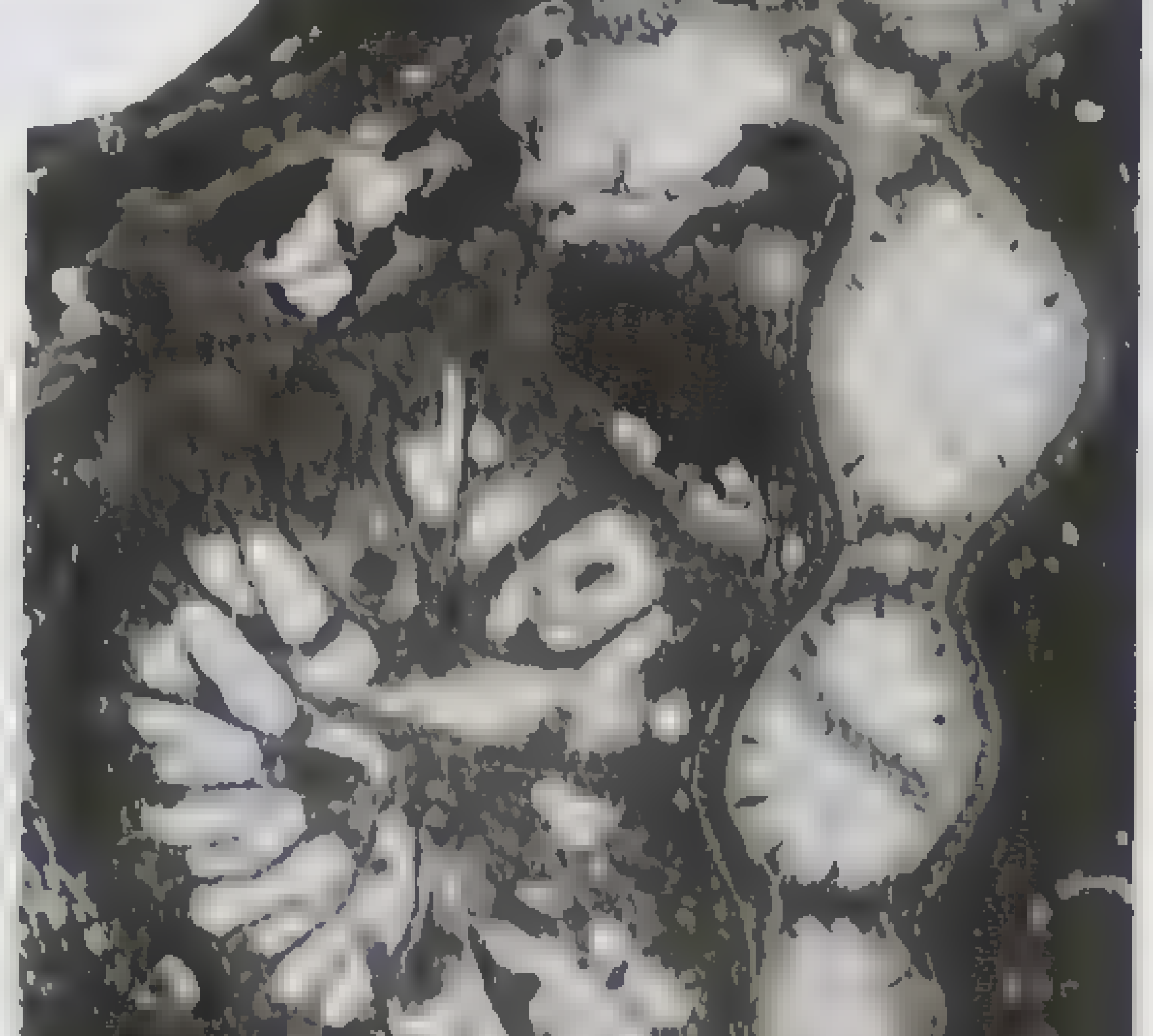
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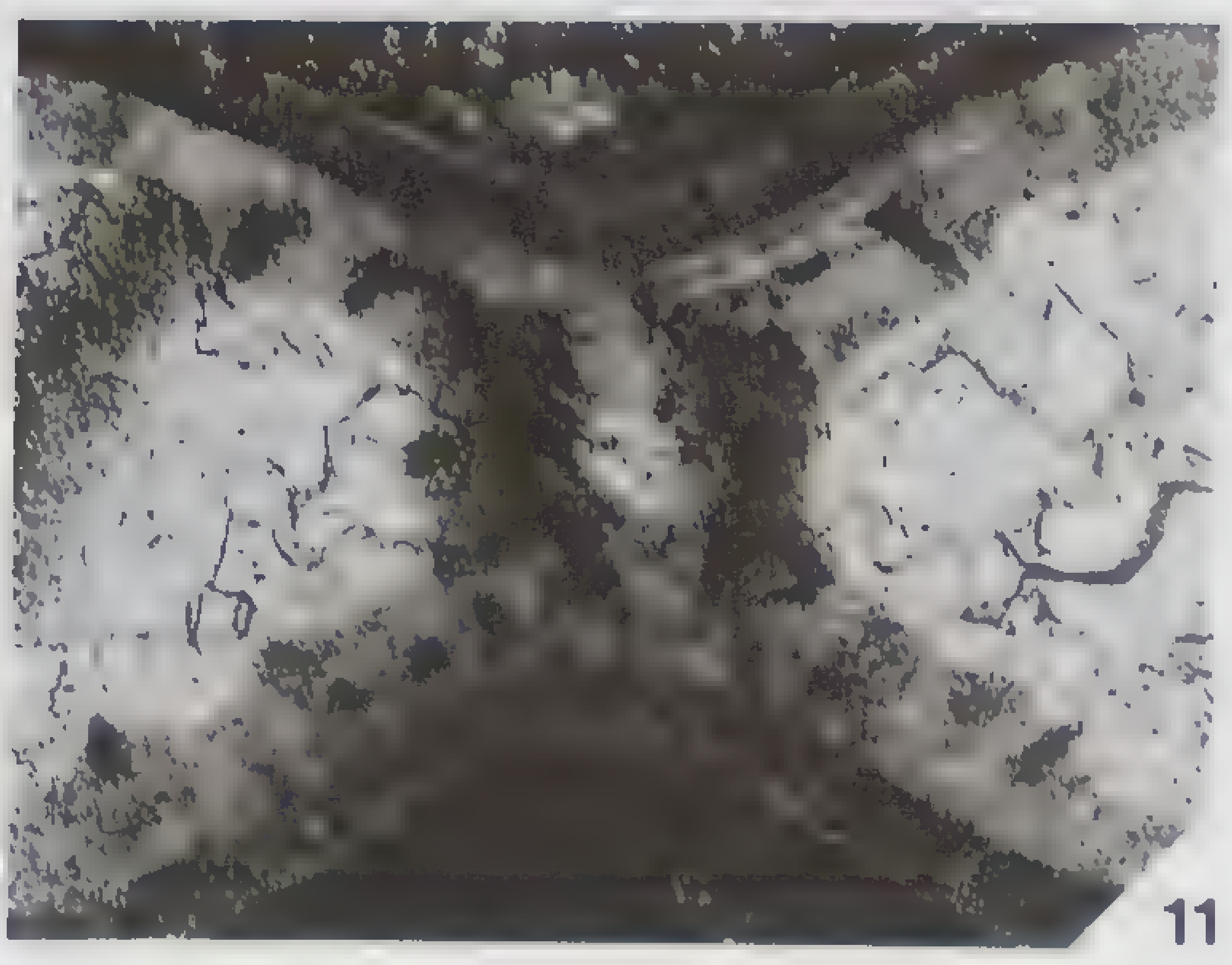
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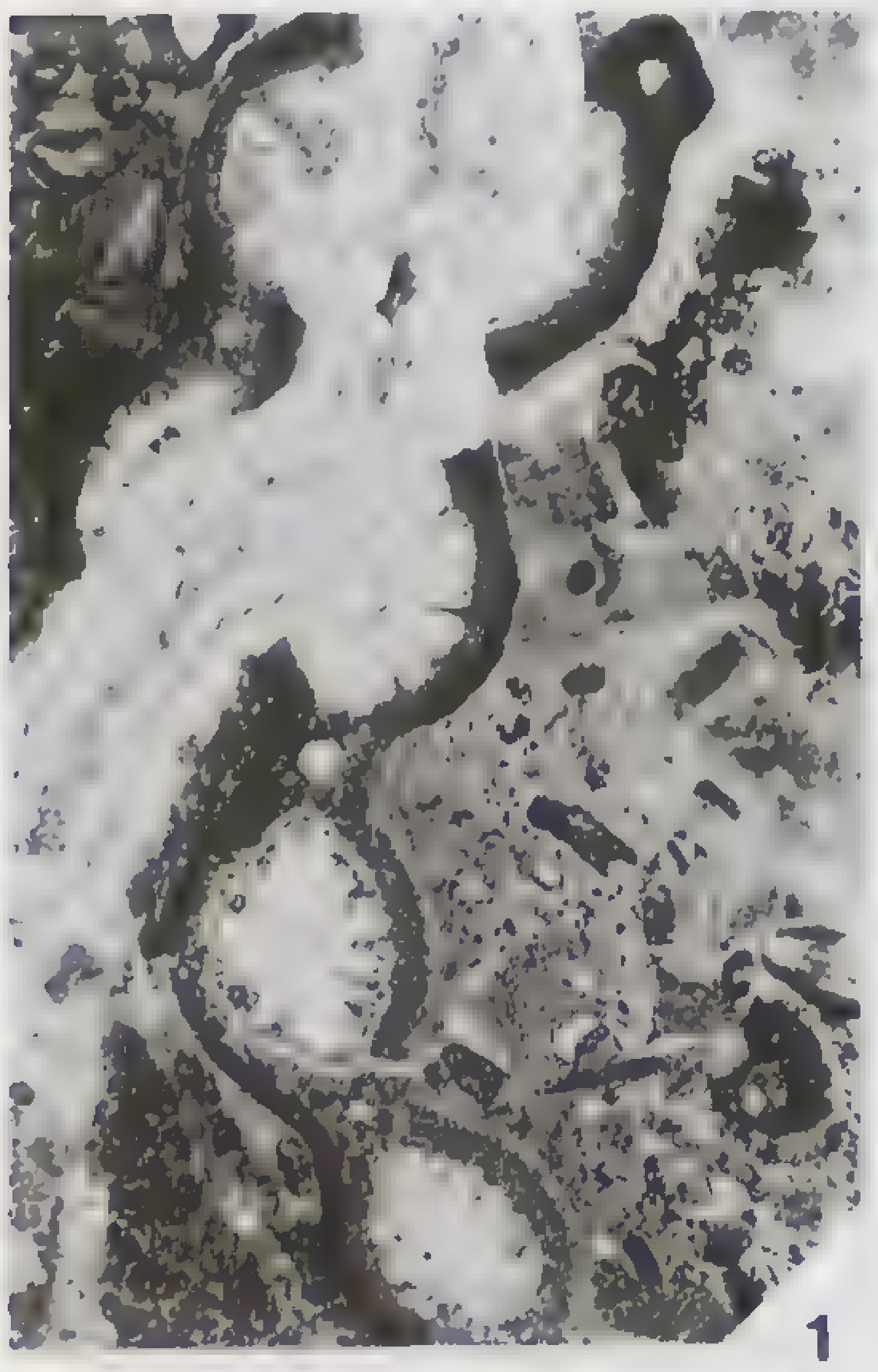

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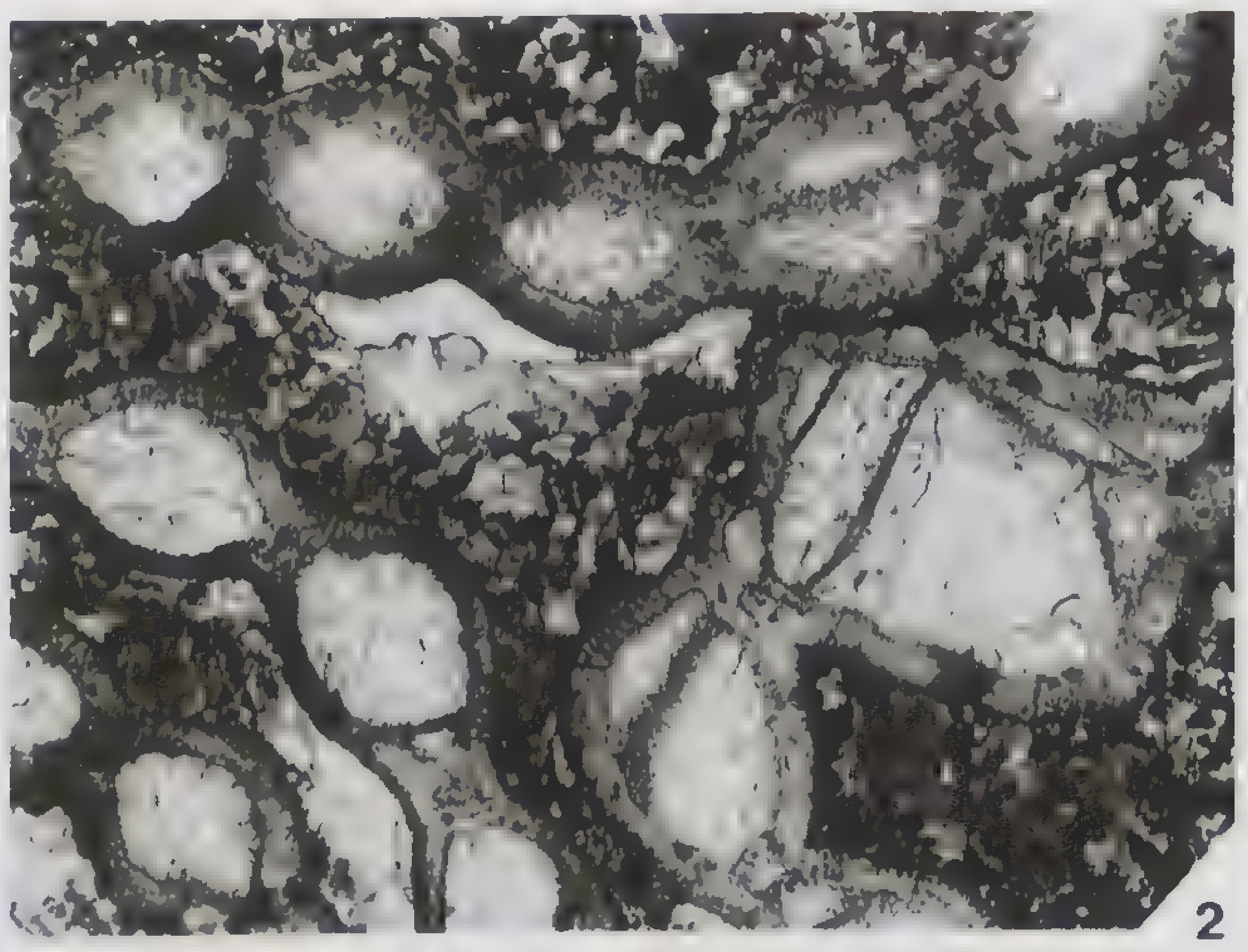

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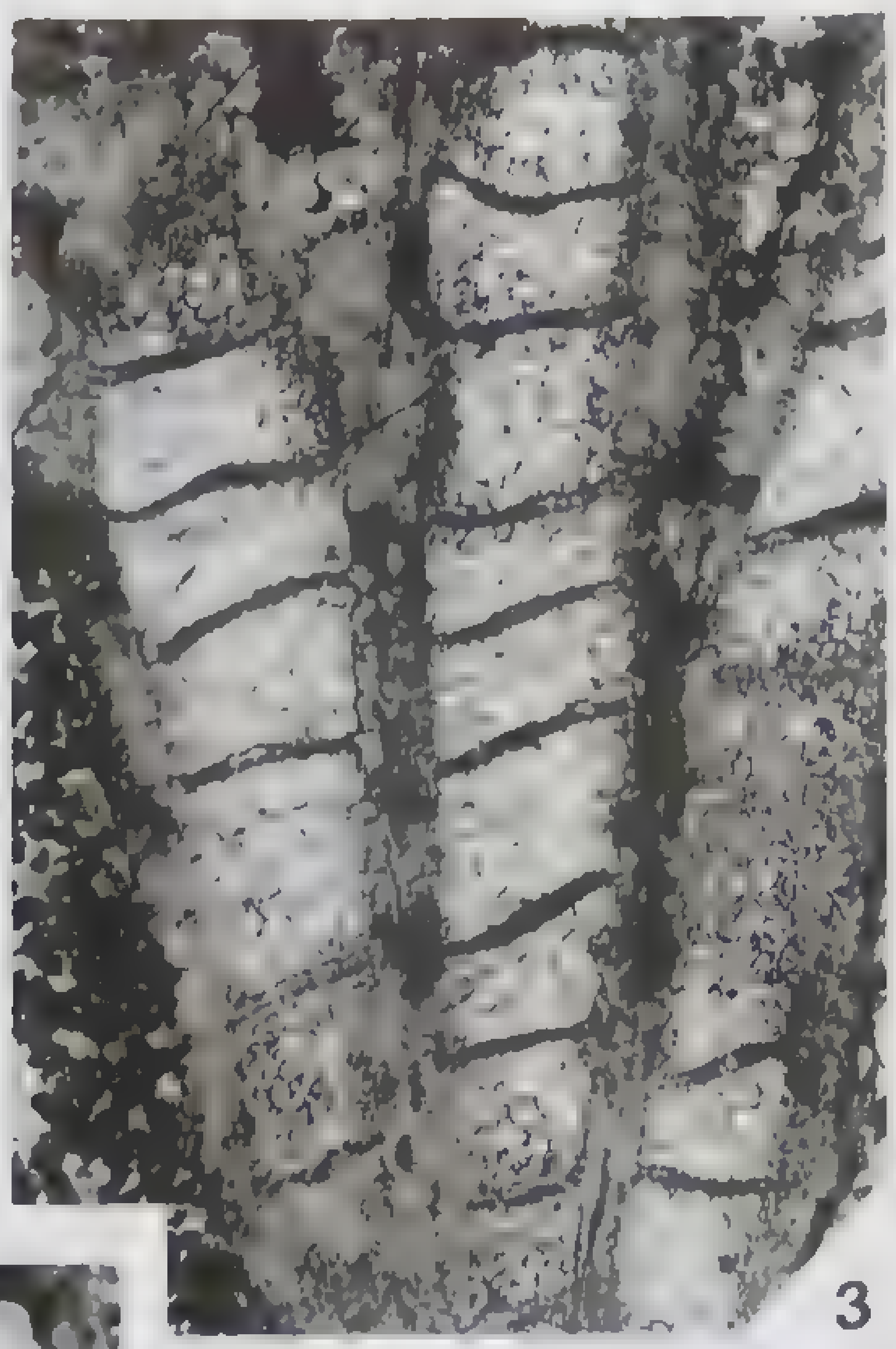

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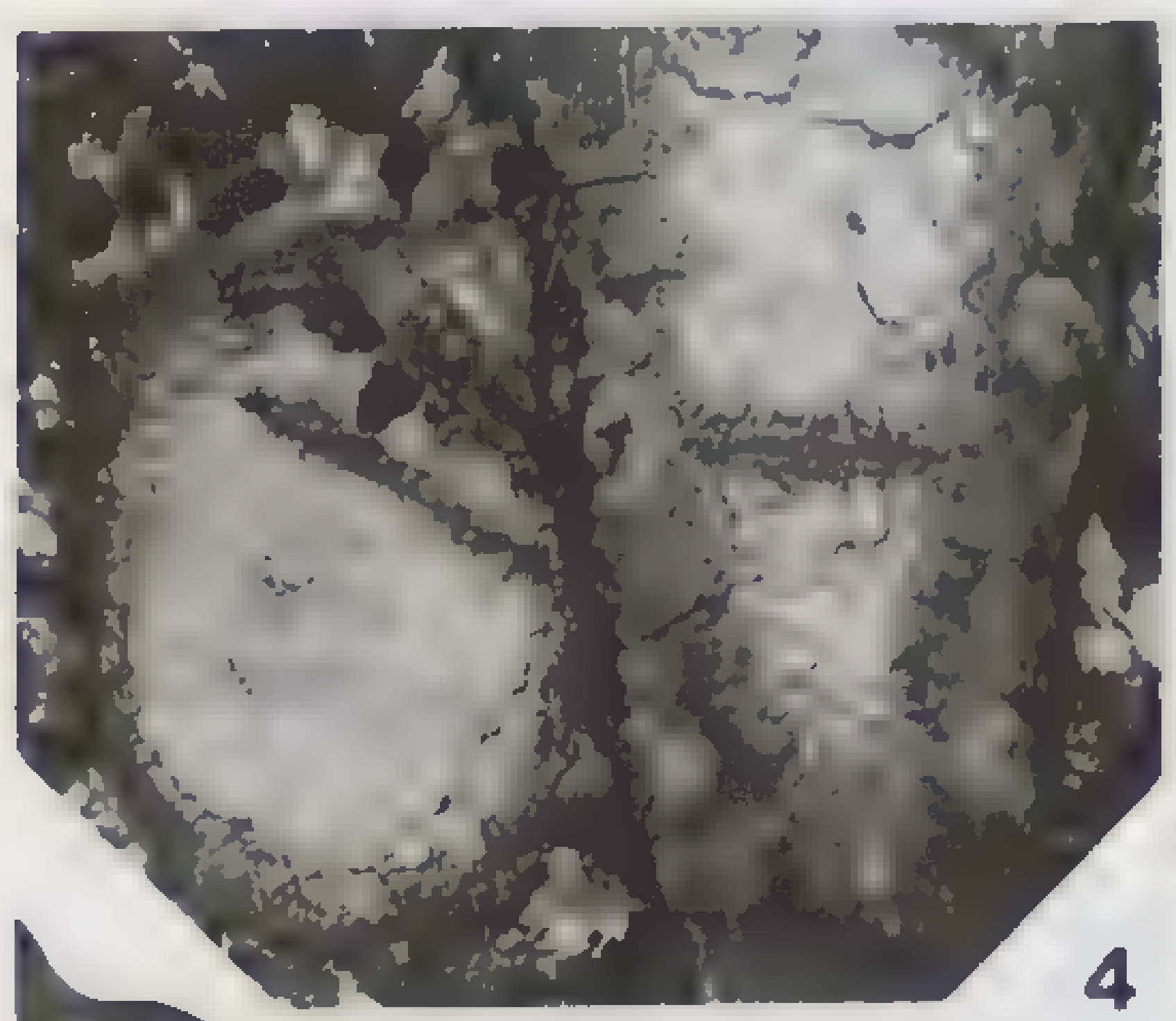

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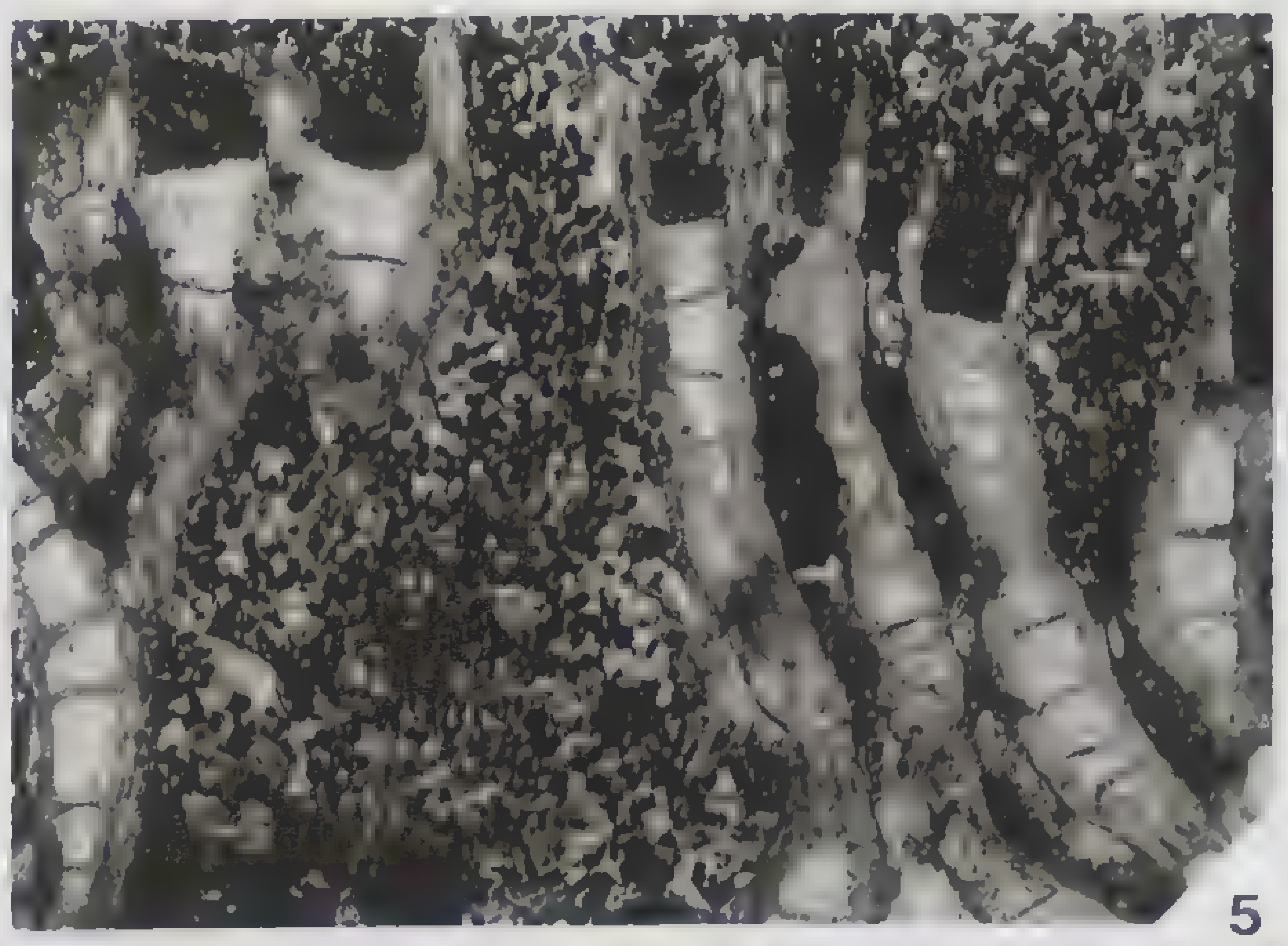

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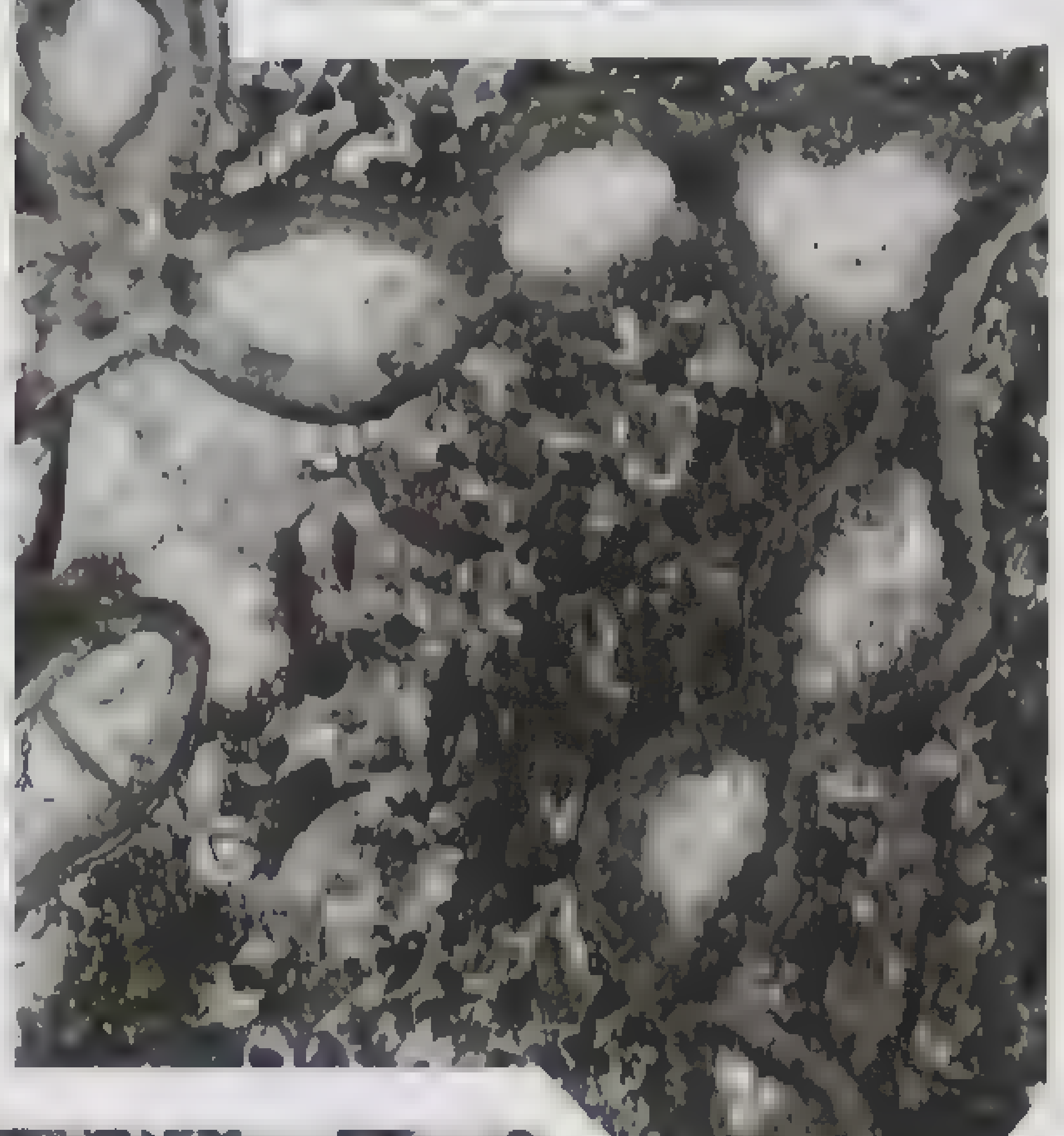

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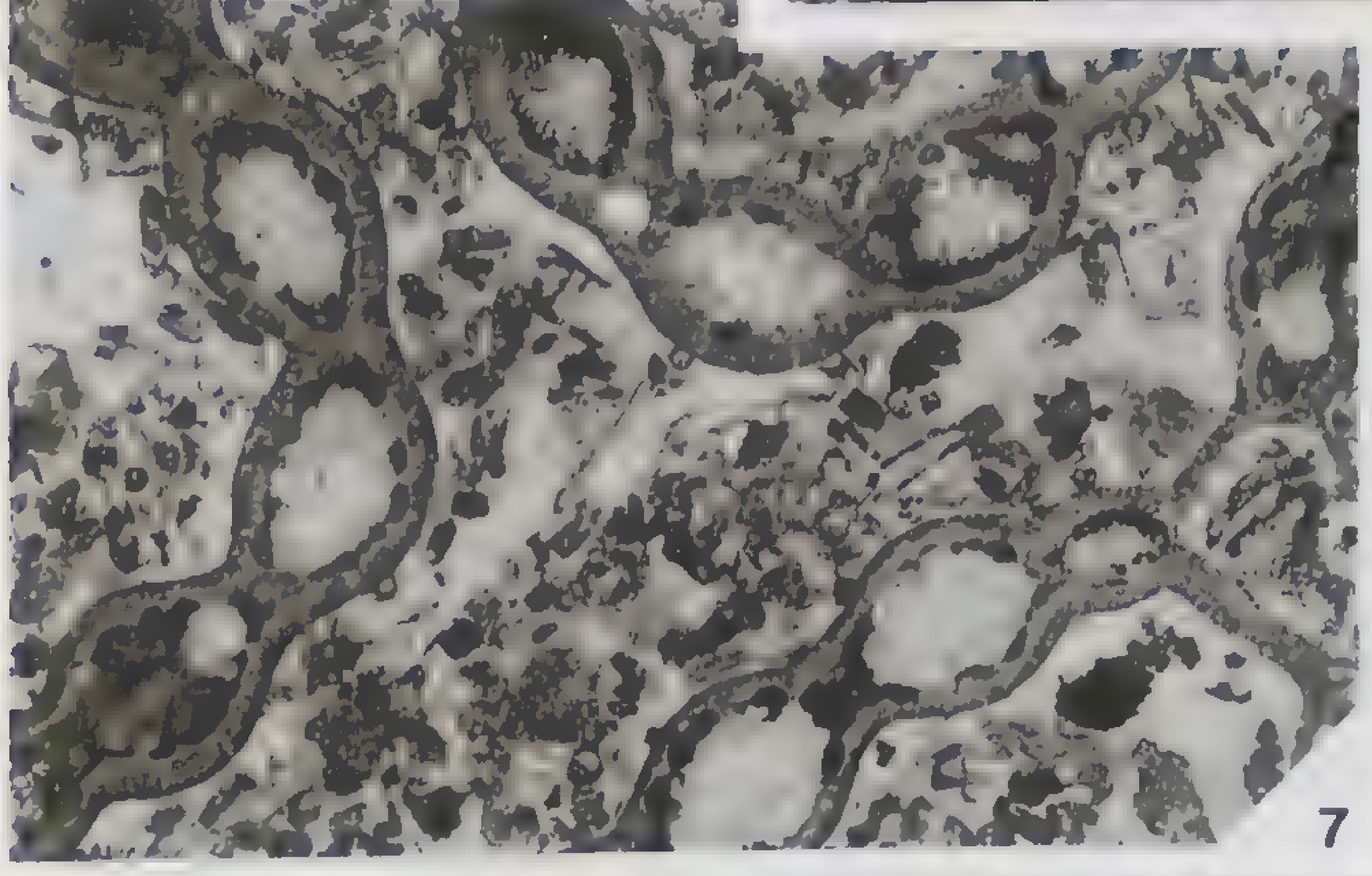

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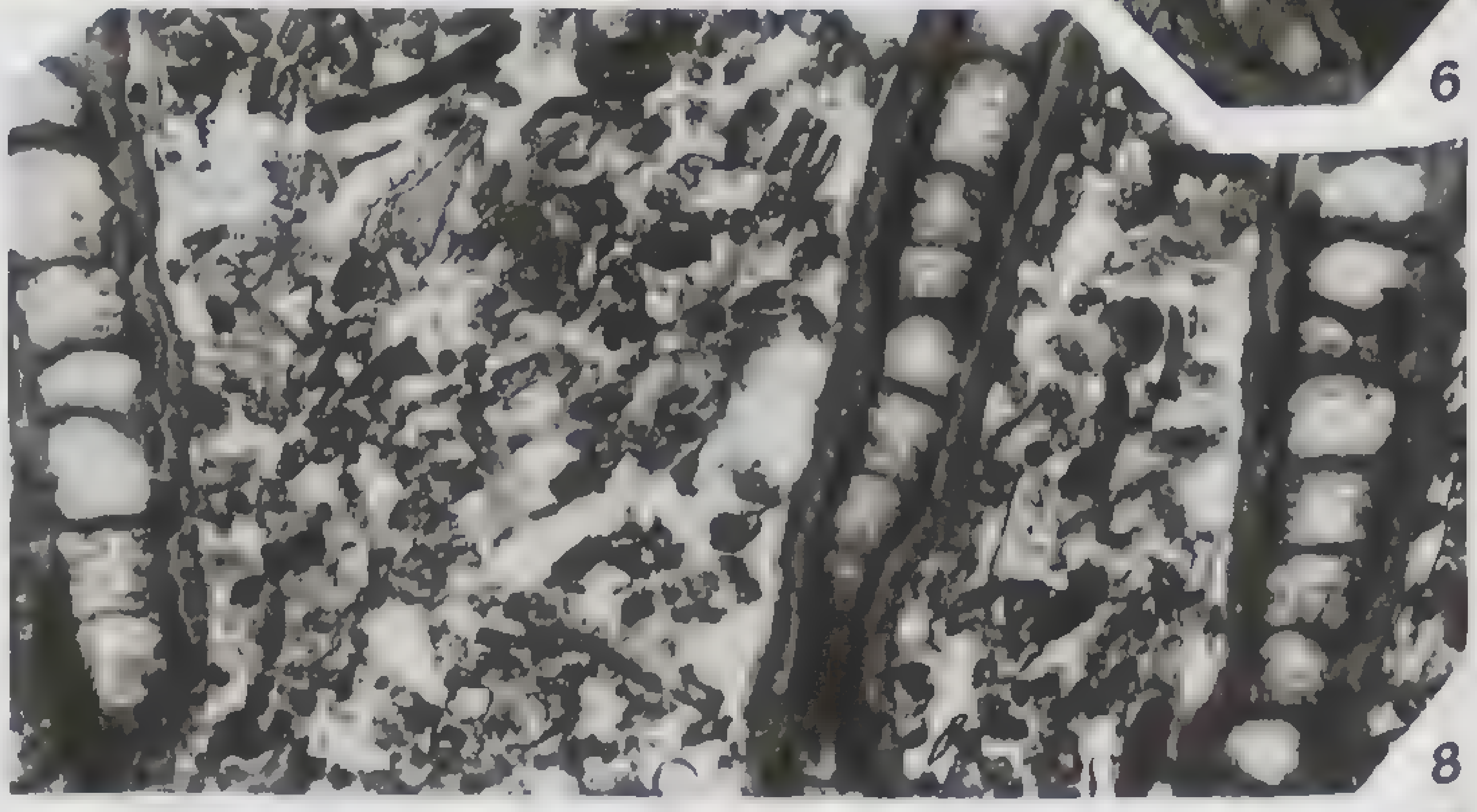

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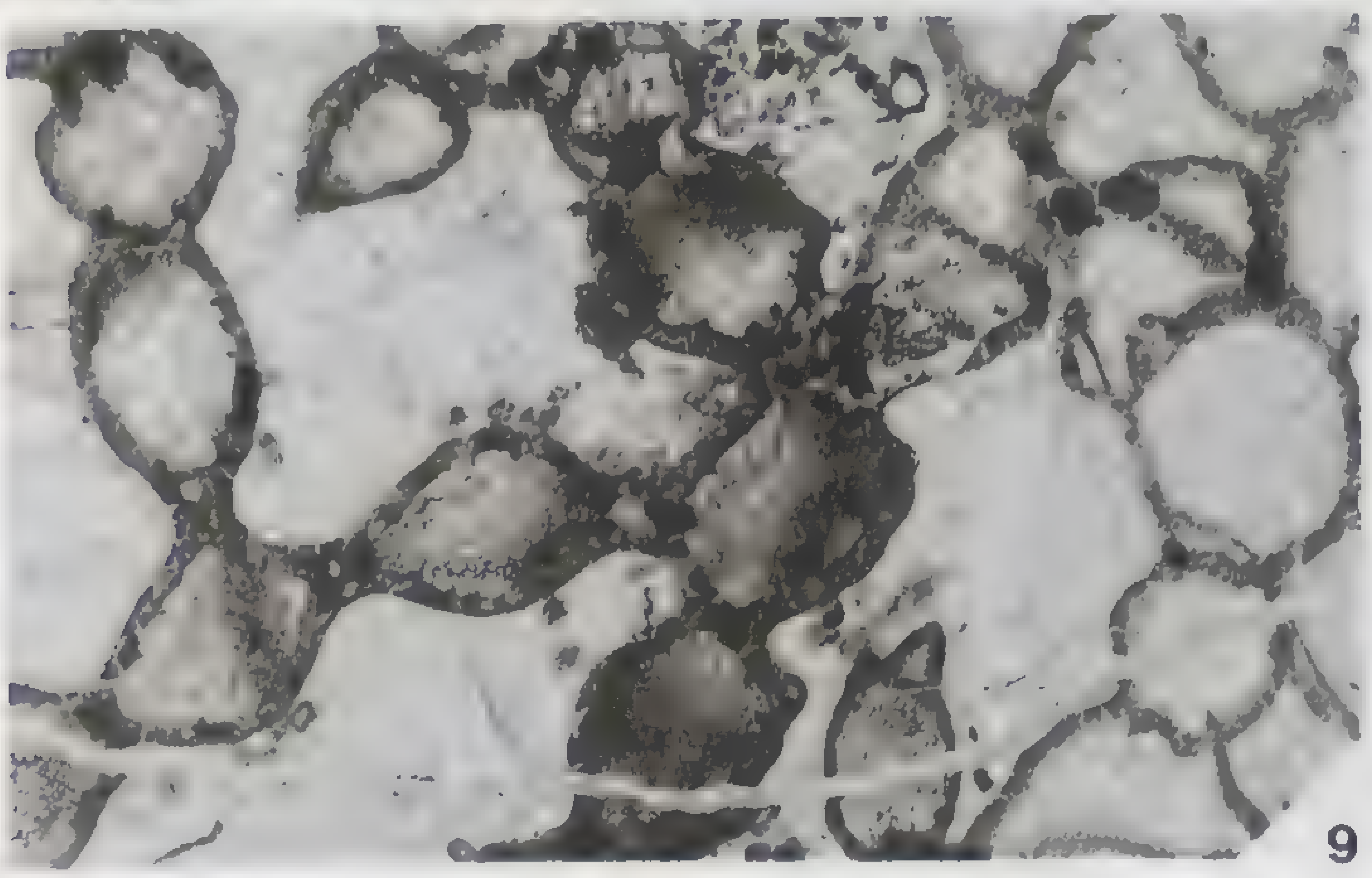

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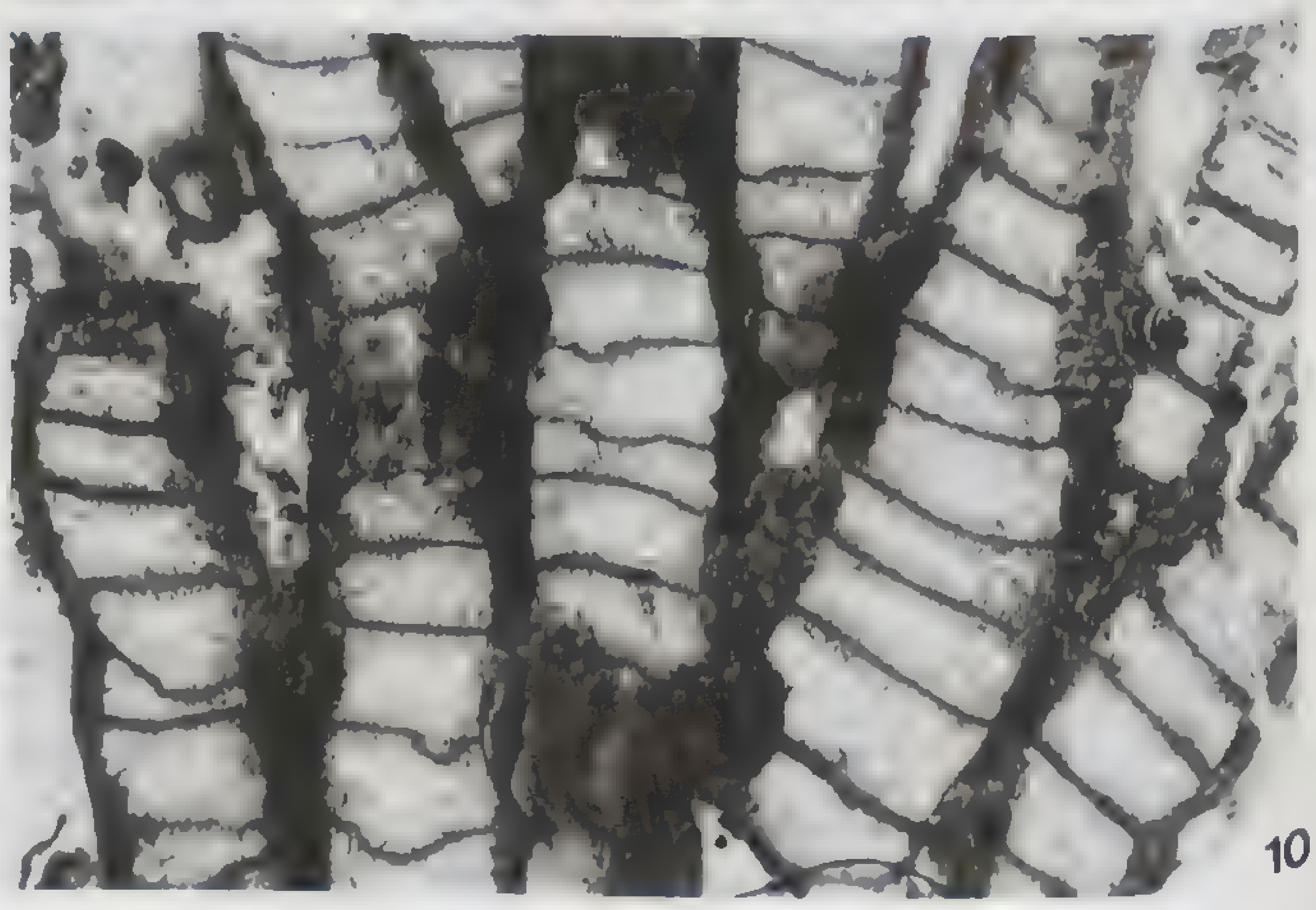

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EXPLANATION OF PLATE 10

Figure Page

1–10. ***Halysites alexandricus,*** new species 67

[1, Cason Shale, Section-interval 33-1 (Buffalo River); 2–6, Leemon Formation, Section-interval 31-1 (Thebes North); 7–10, Kissenger Limestone Member, Bryant Knob Formation, Section-interval 15-1 (Calumet).]

1. USNM 485795: transverse section showing rank cut by a vein, ×8.

2–4. USNM 485781 (holotype): 2, transverse section showing "megacorallite" (right of center), ×8; 3, longitudinal section, ×8; 4, longitudinal section (note probable encrusting tentaculitid on left), ×15.

5, 6. USNM 485796: 5, longitudinal section showing calices, ×5; 6, transverse section, ×8.

7, 8. USNM 485783 (paratype): 7, transverse section, ×8; 8, longitudinal section, ×8.

9, 10. USNM 485800a: 9, transverse section (note irregularly shaped corallites on right side), ×8; 10, longitudinal section, ×8.

EXPLANATION OF PLATE 11

Figure Page

1–6. ***Halysites alexandricus,*** new species 67

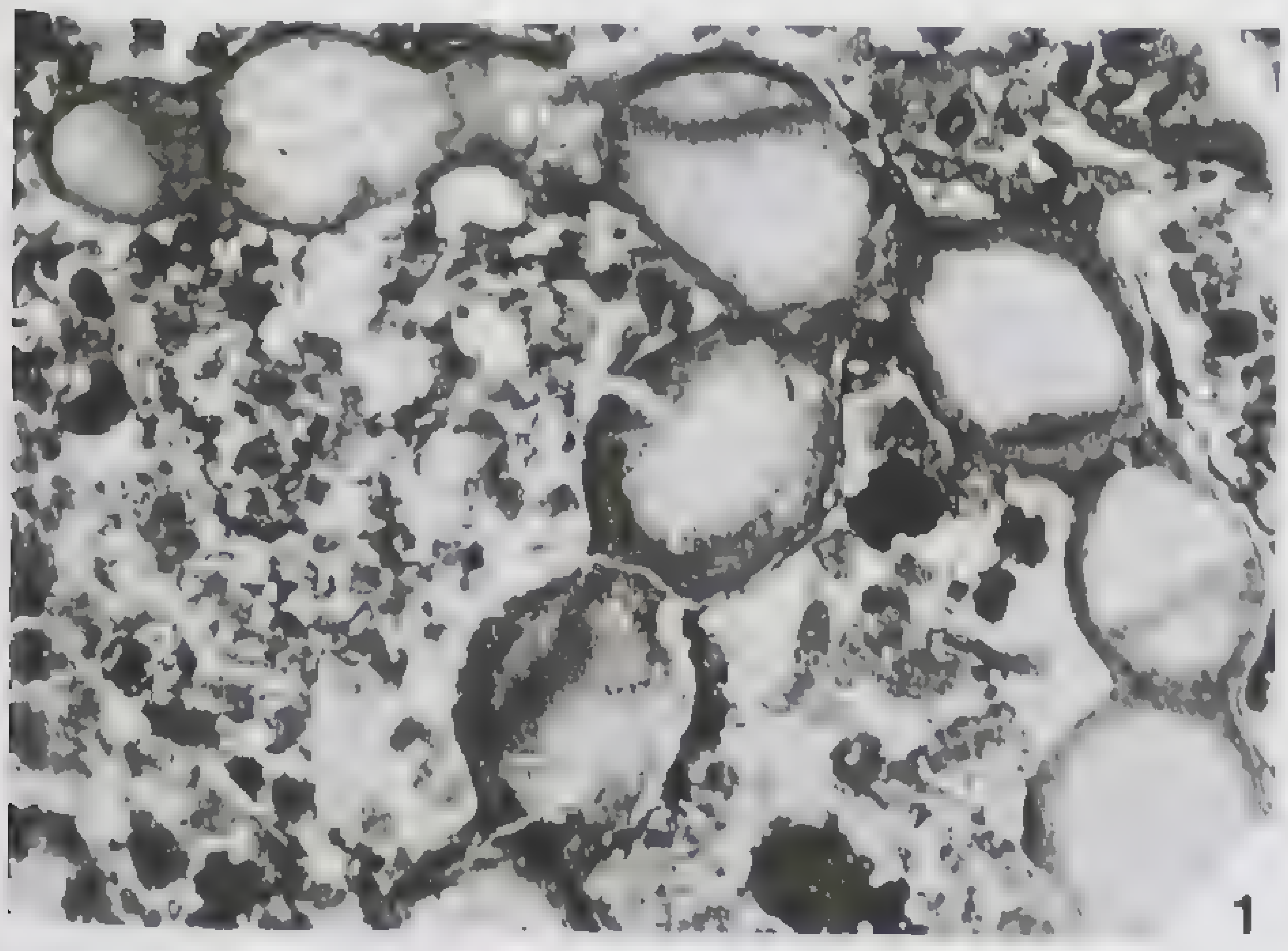
[1, 2, Kissenger Limestone Member, Bryant Knob Formation, Section-interval 14-1 (Higginbotham Farm); 3, 4, Wilhelmi Formation, Section-interval 37-1 (Essex); 5, 6, Wilhelmi Formation, 3.2 km south of Channahon, Illinois.]

1, 2. USNM 485804: 1, transverse section, ×8; 2, longitudinal section, ×8.
3, 4. USNM 485809: 3, transverse section, ×8; 4, longitudinal section, ×8.
5, 6. UI X-8723 (paratype): 5, transverse section, ×8; 6, longitudinal section, ×8.

7–9. ***Halysites*** species cf. ***H. alexandricus,*** new species 72

[7–9, Sexton Creek Limestone, Sexton Creek, Illinois.]

7–9. UI C-1346a: 7, transverse section, ×8; 8, transverse section, ×20; 9, longitudinal section, ×8.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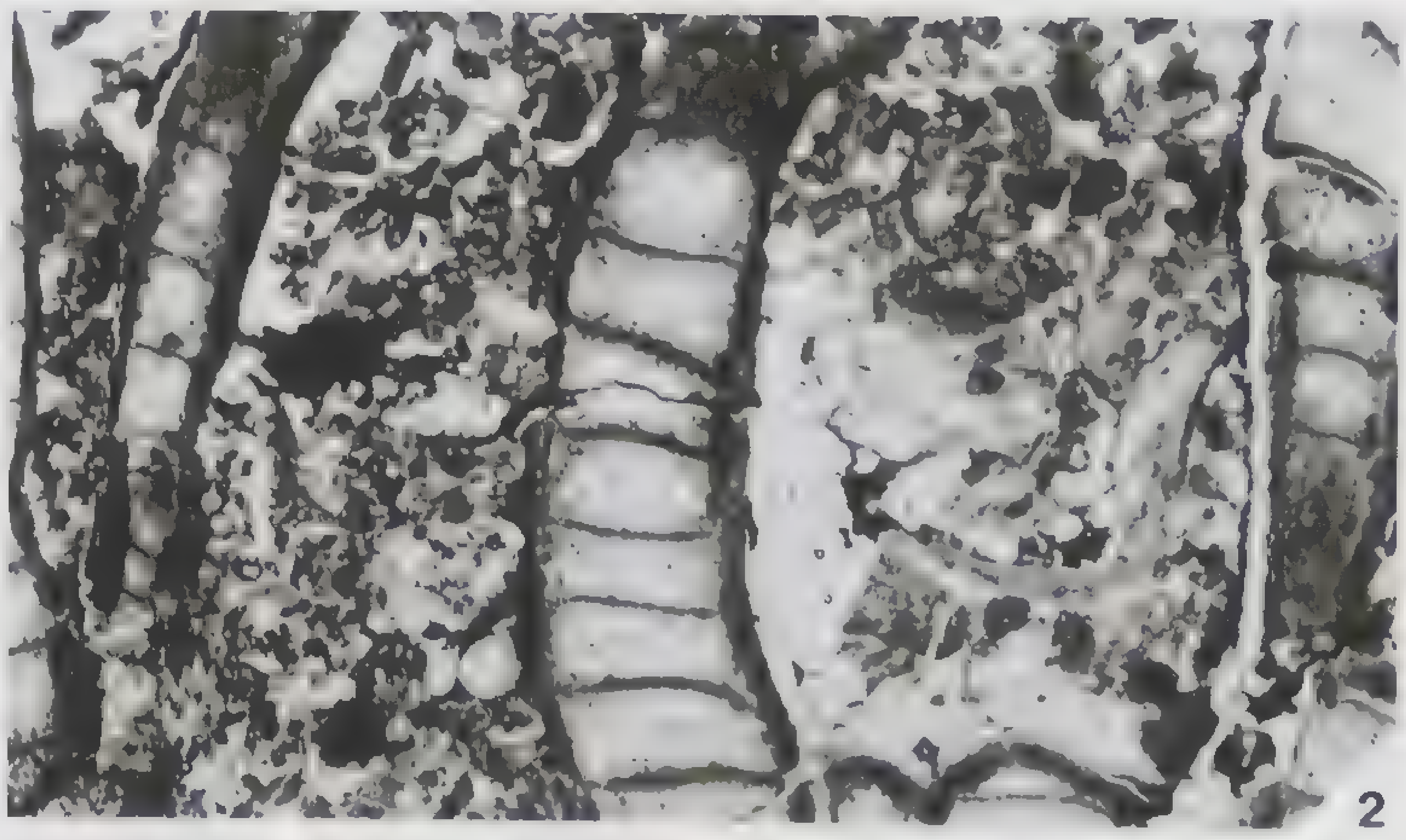
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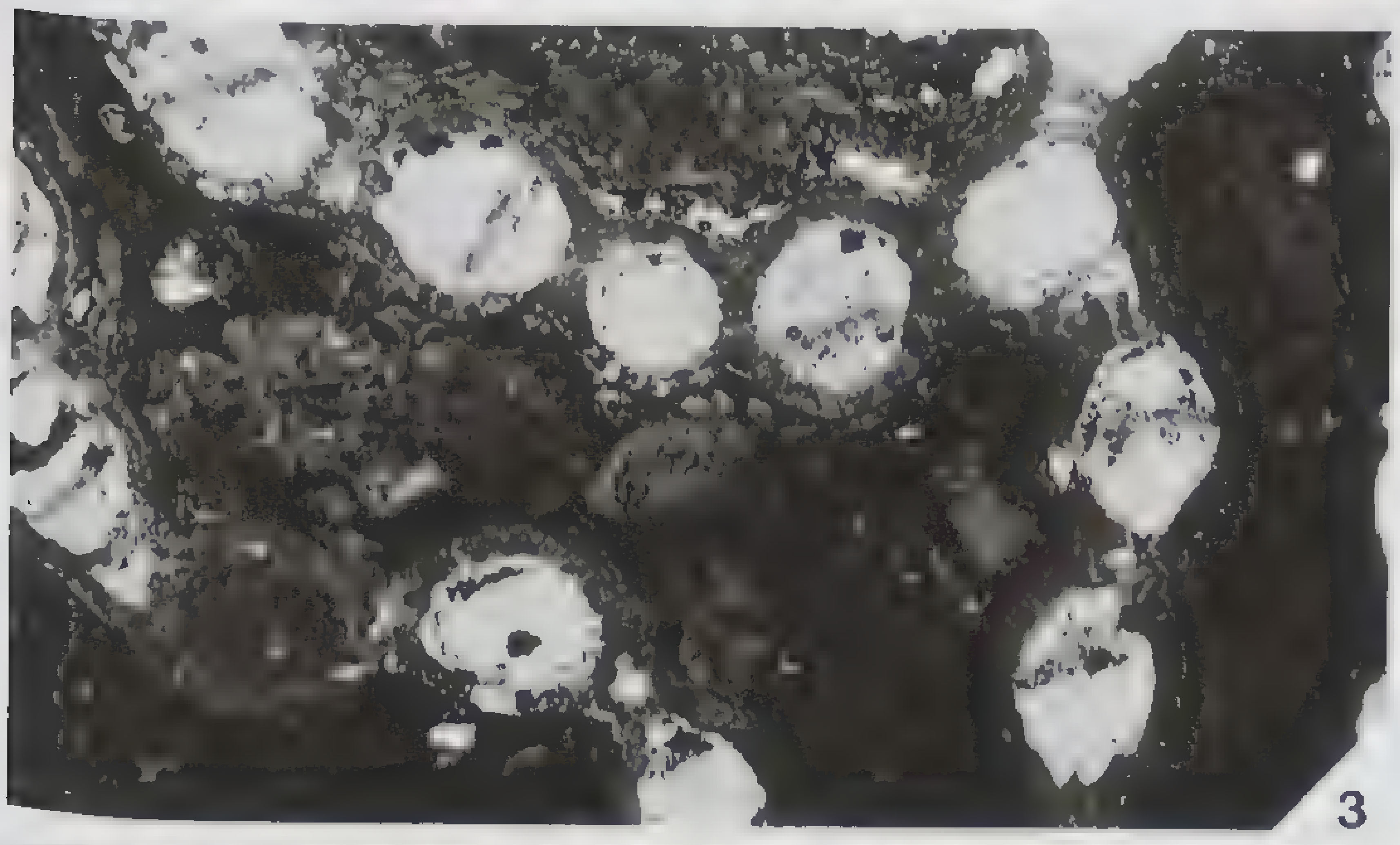
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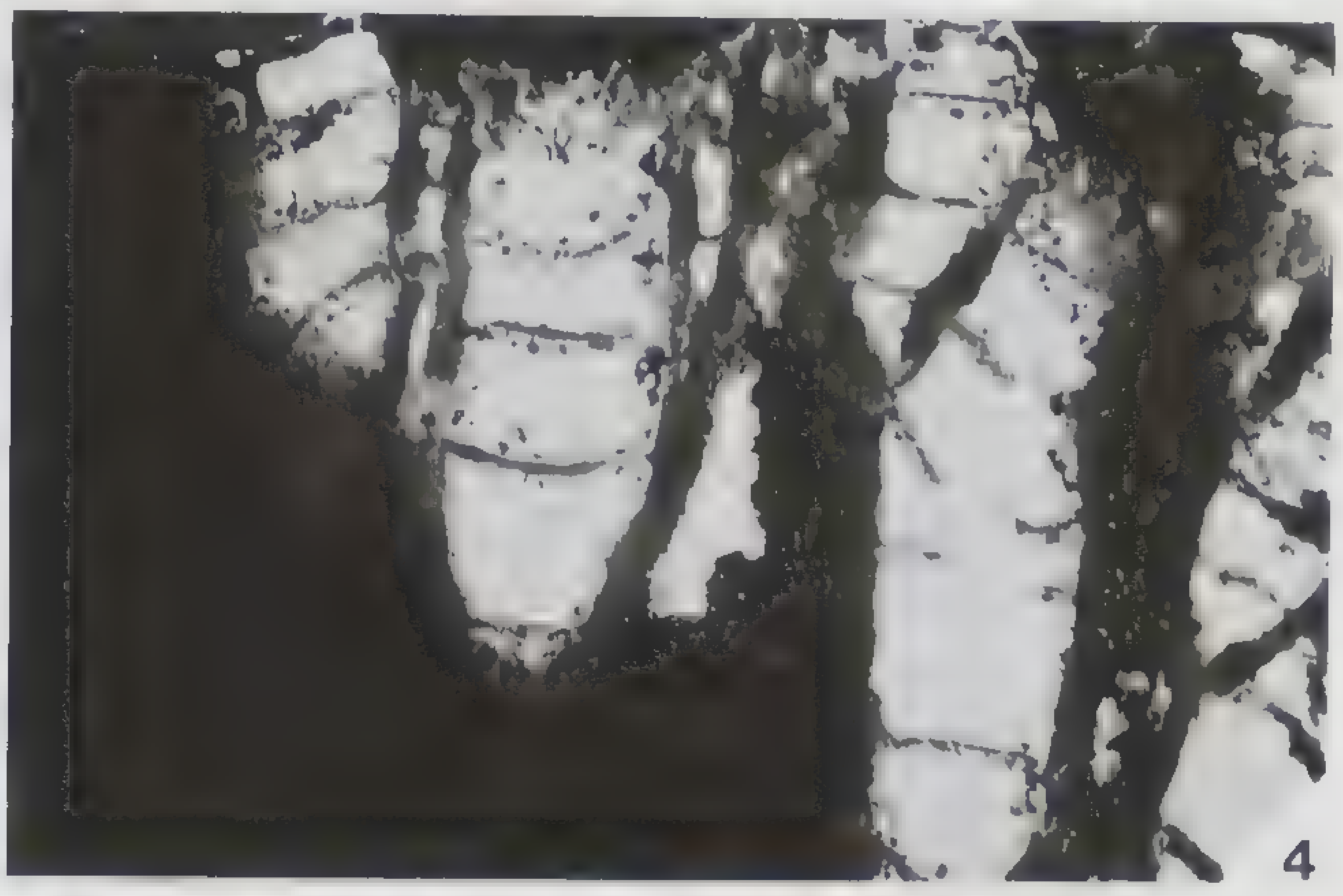
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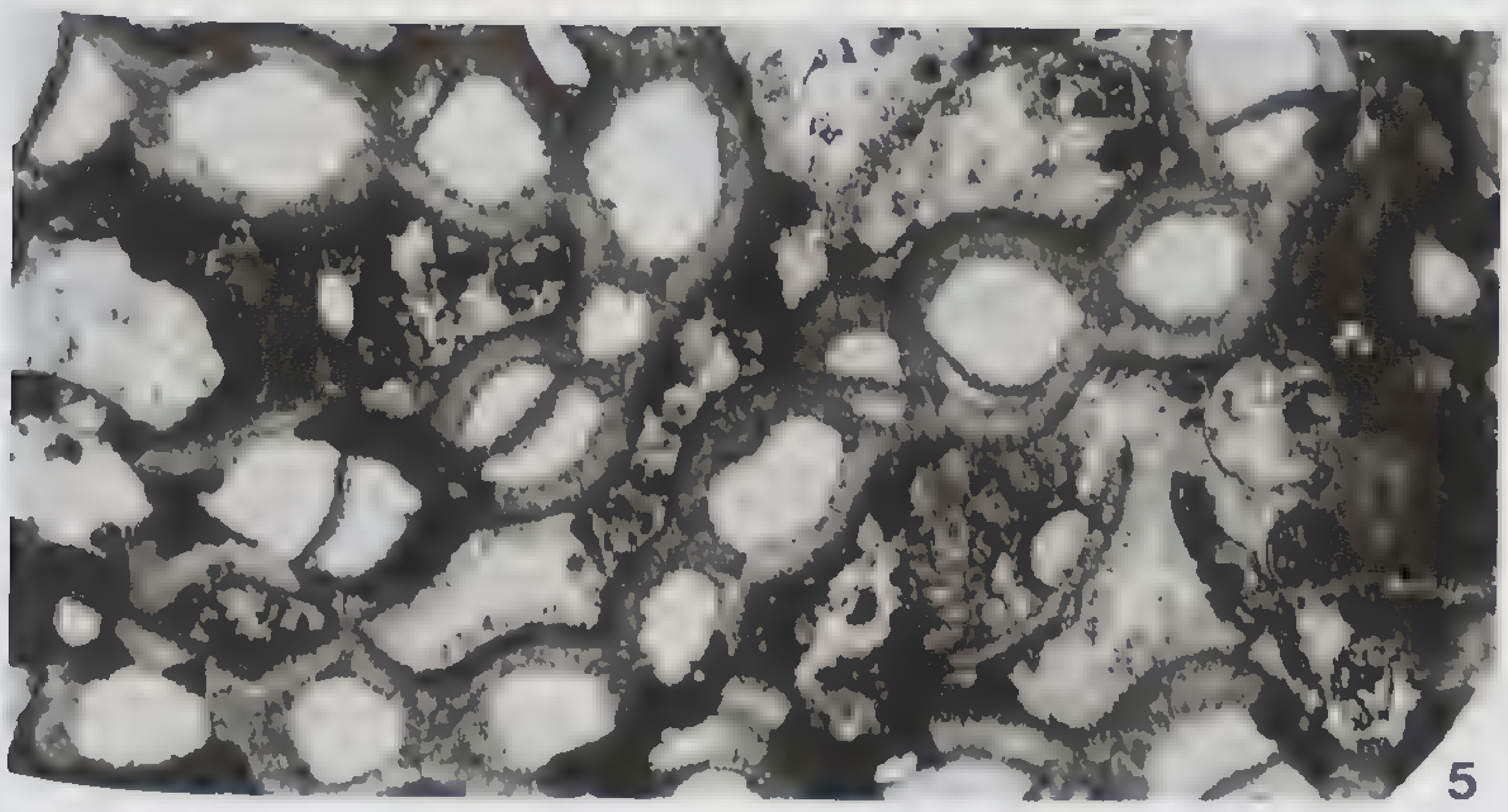
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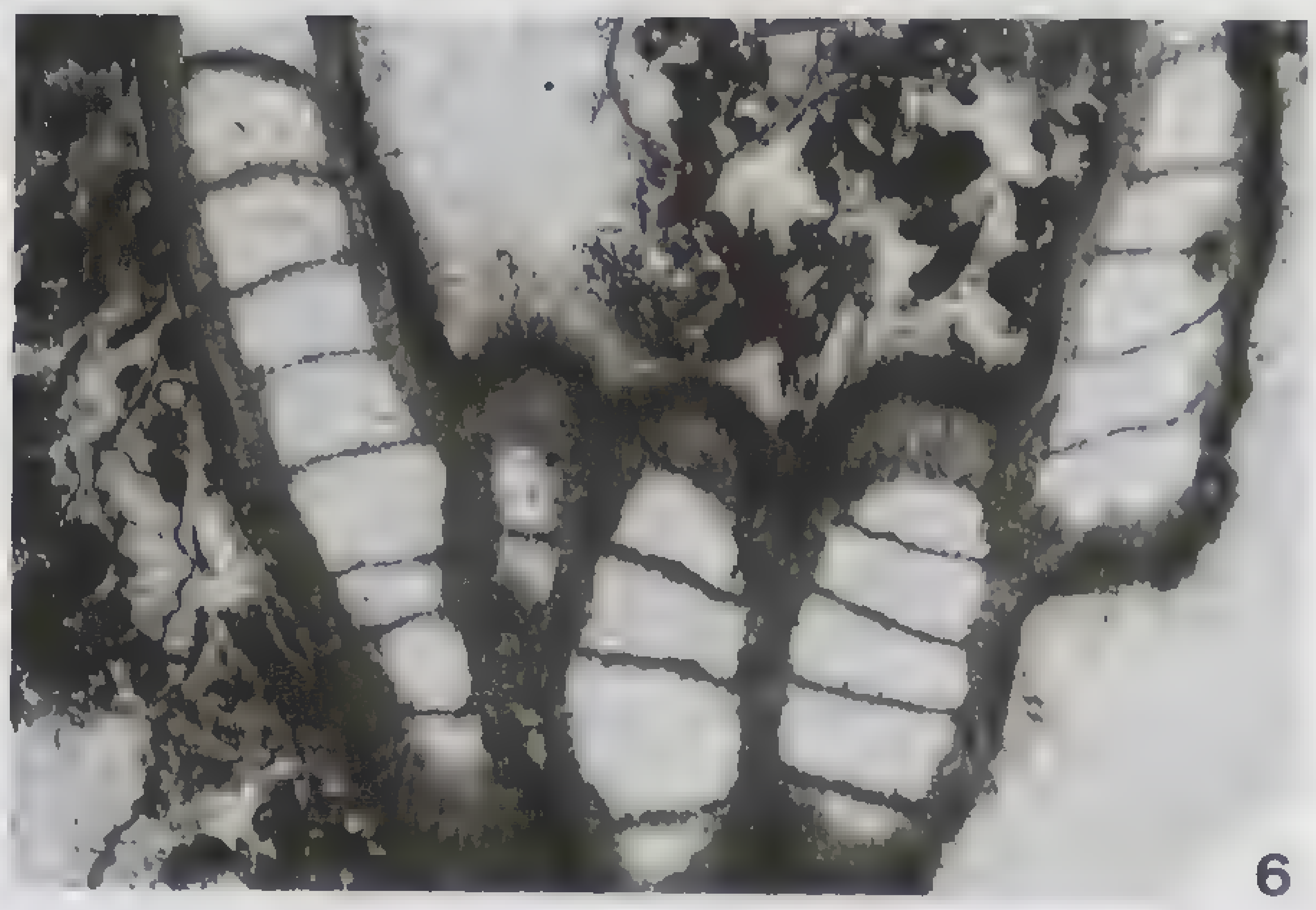
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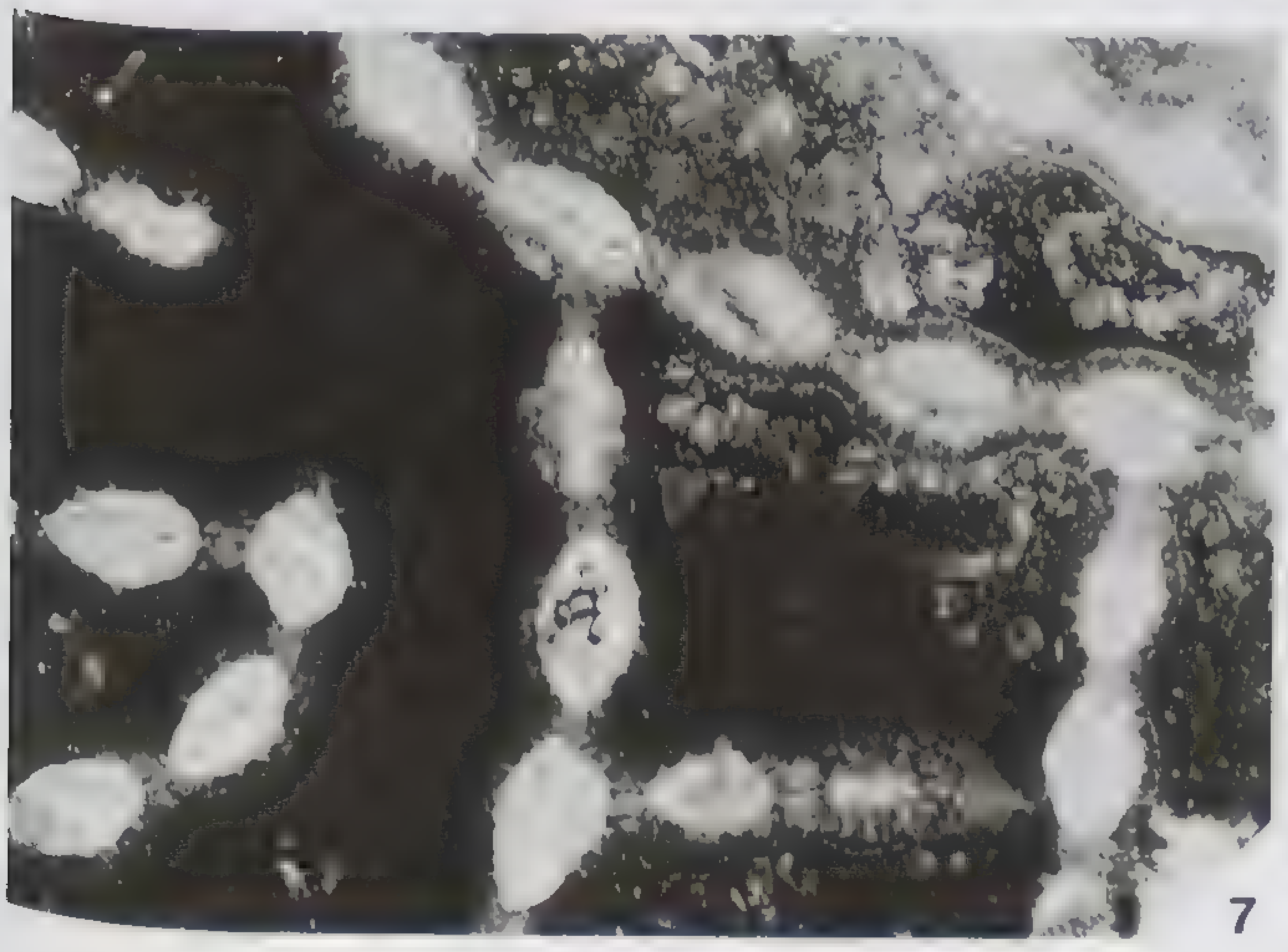
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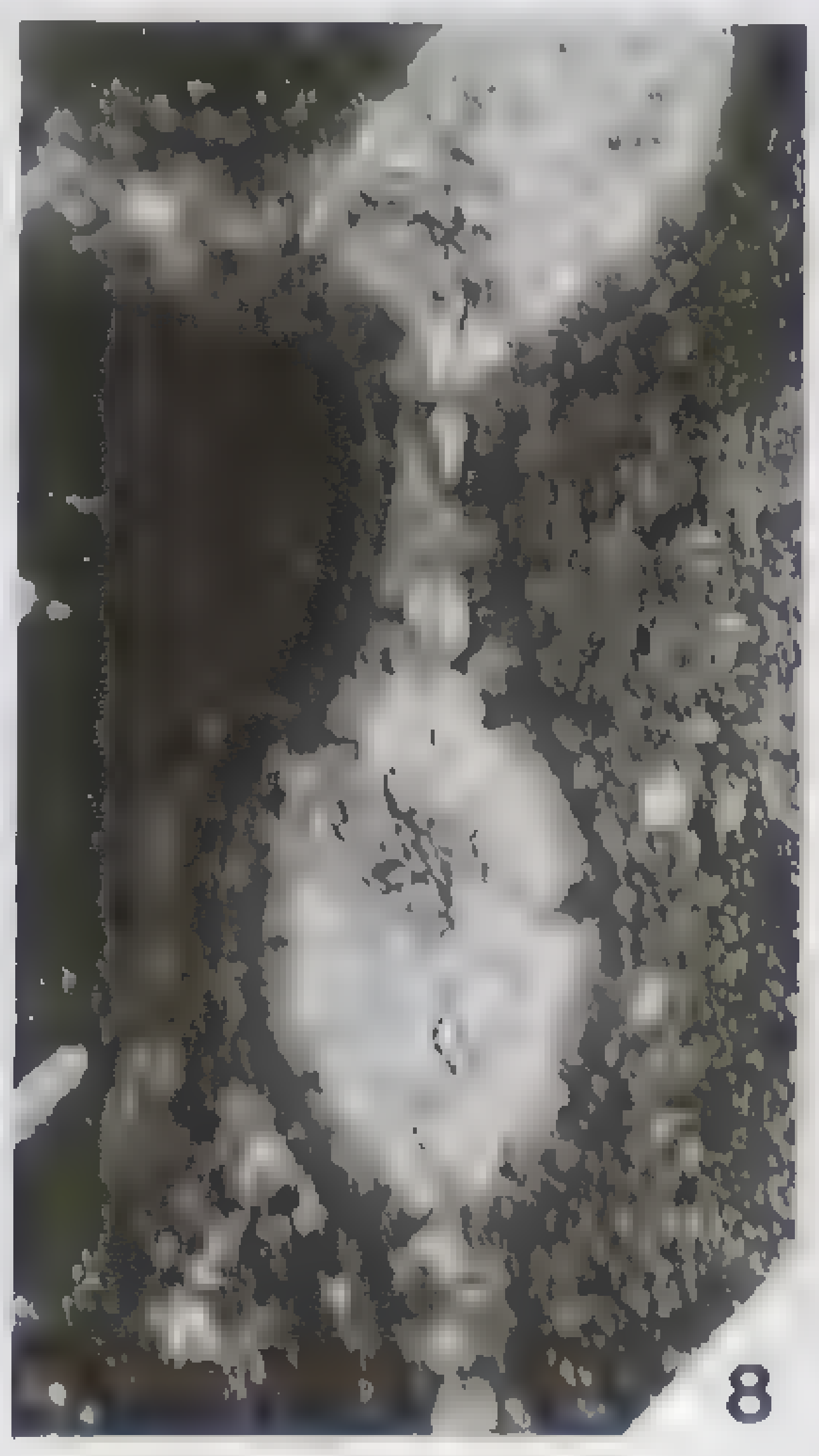
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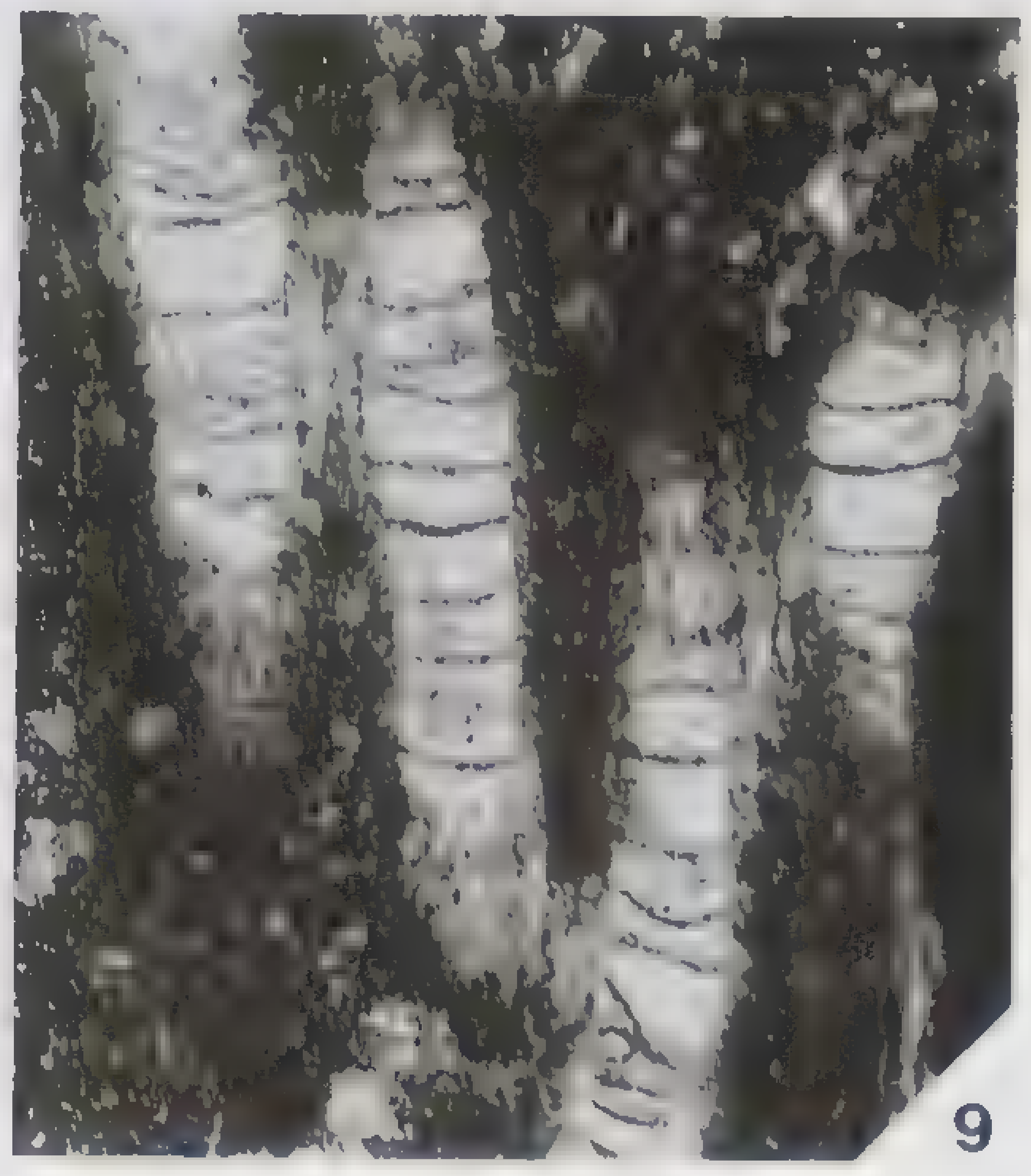
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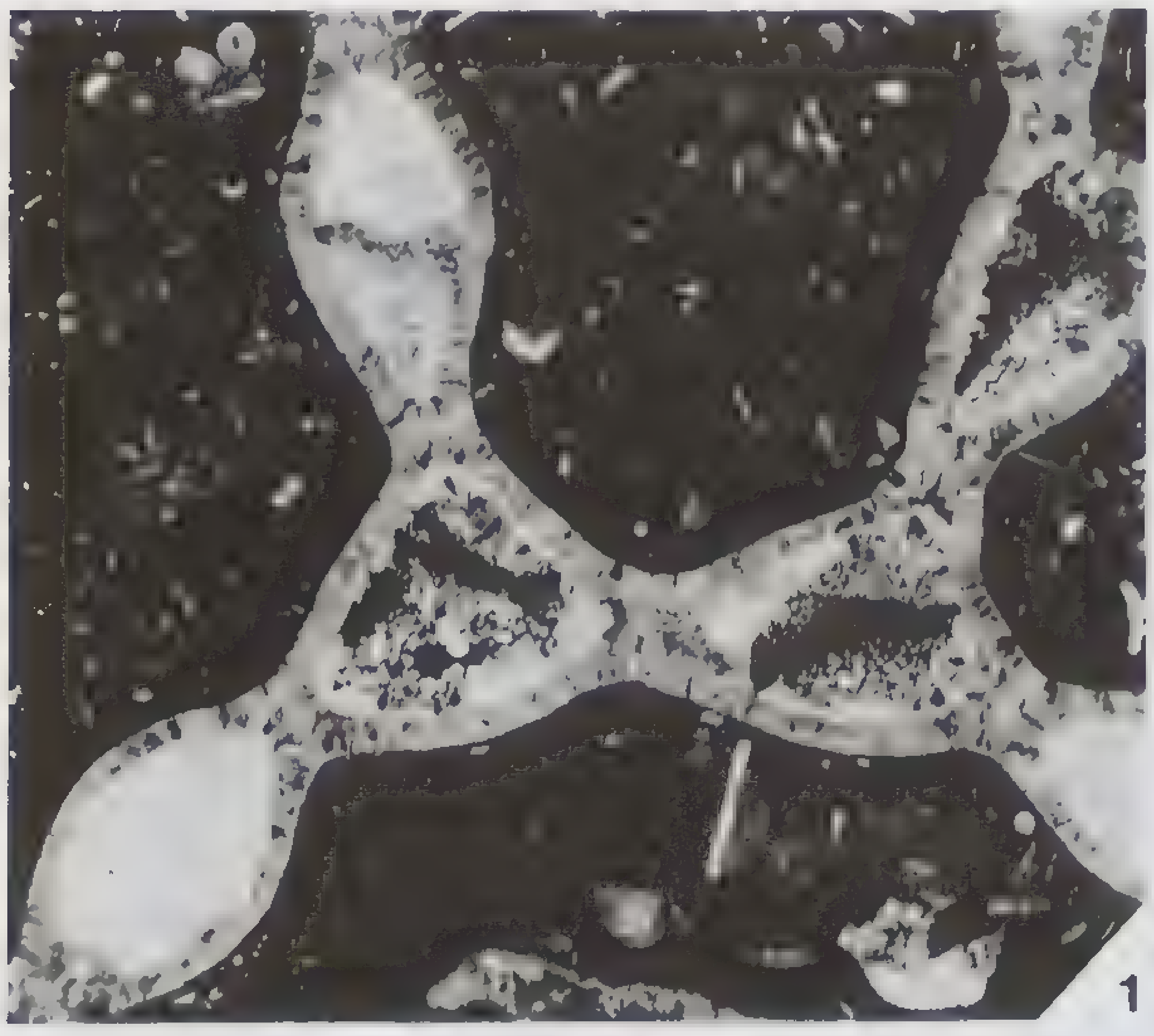
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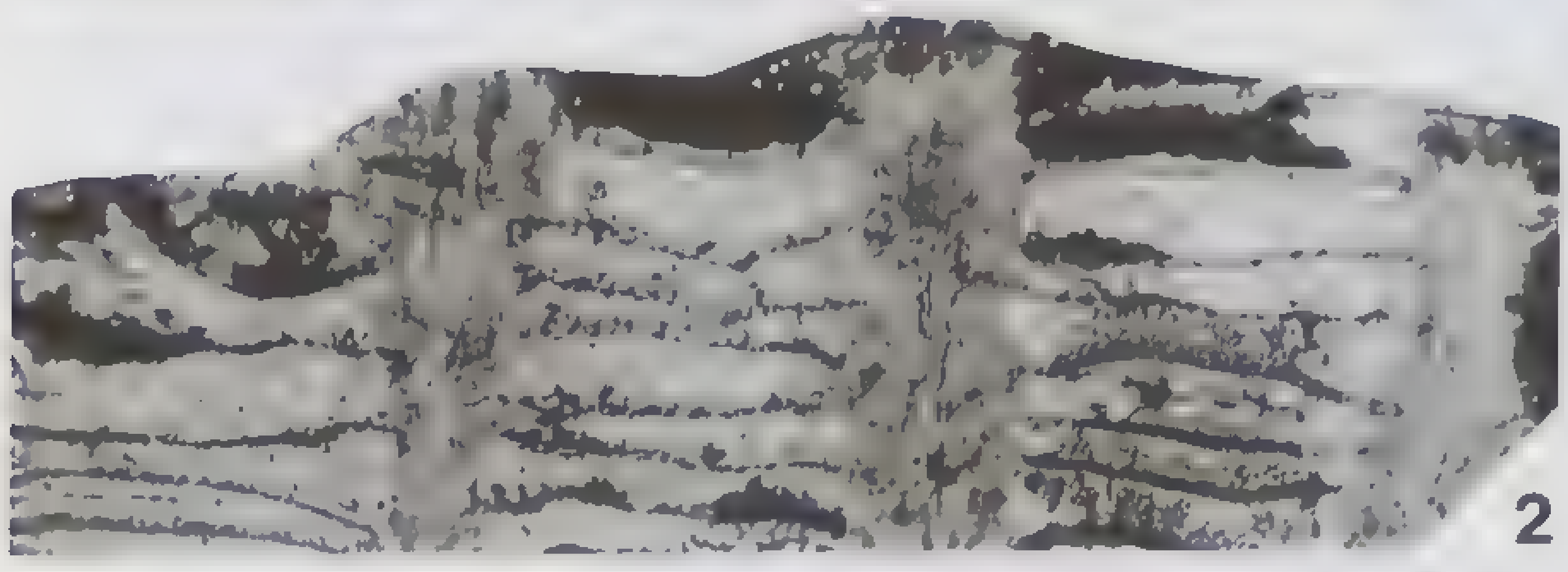
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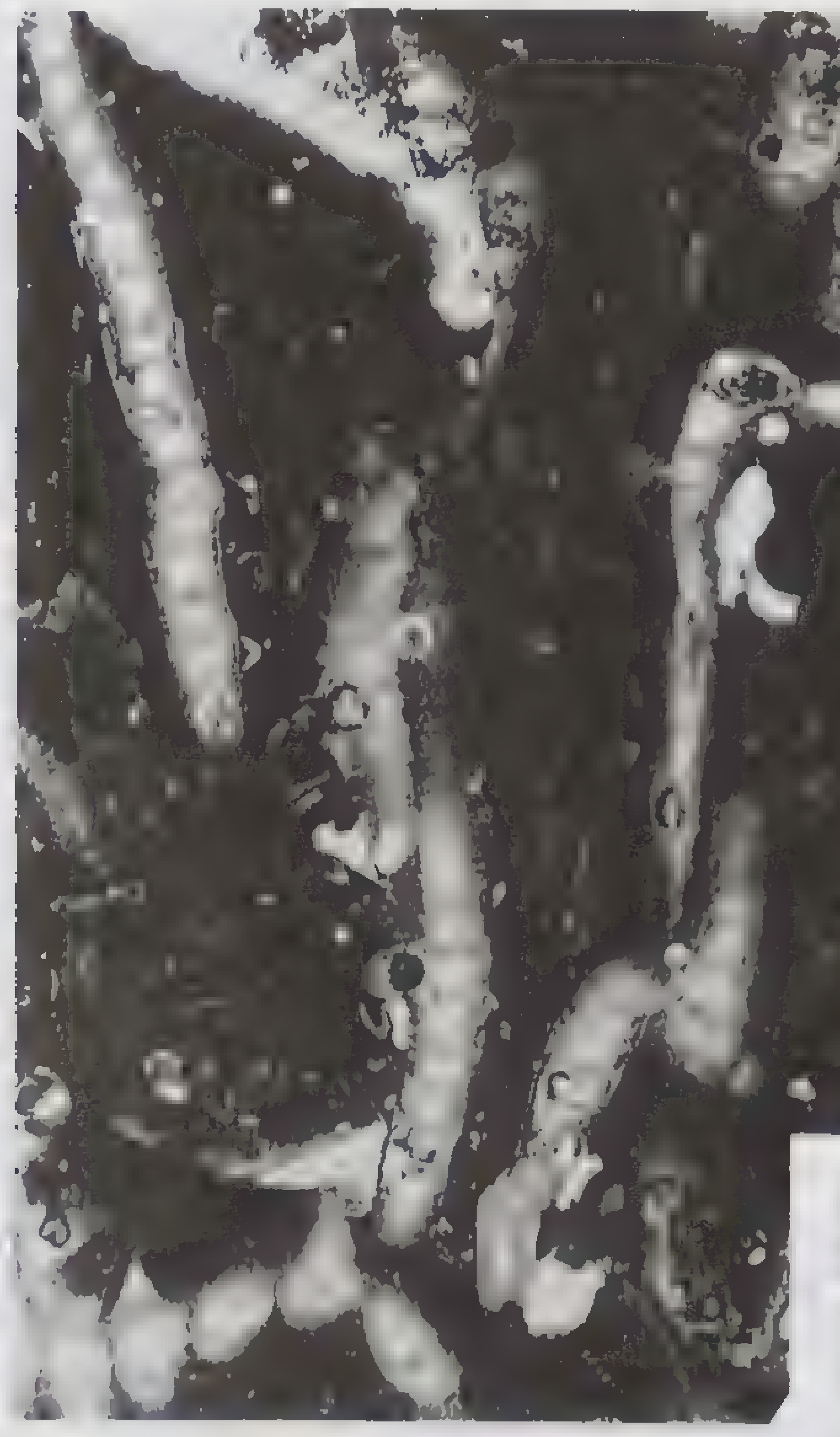
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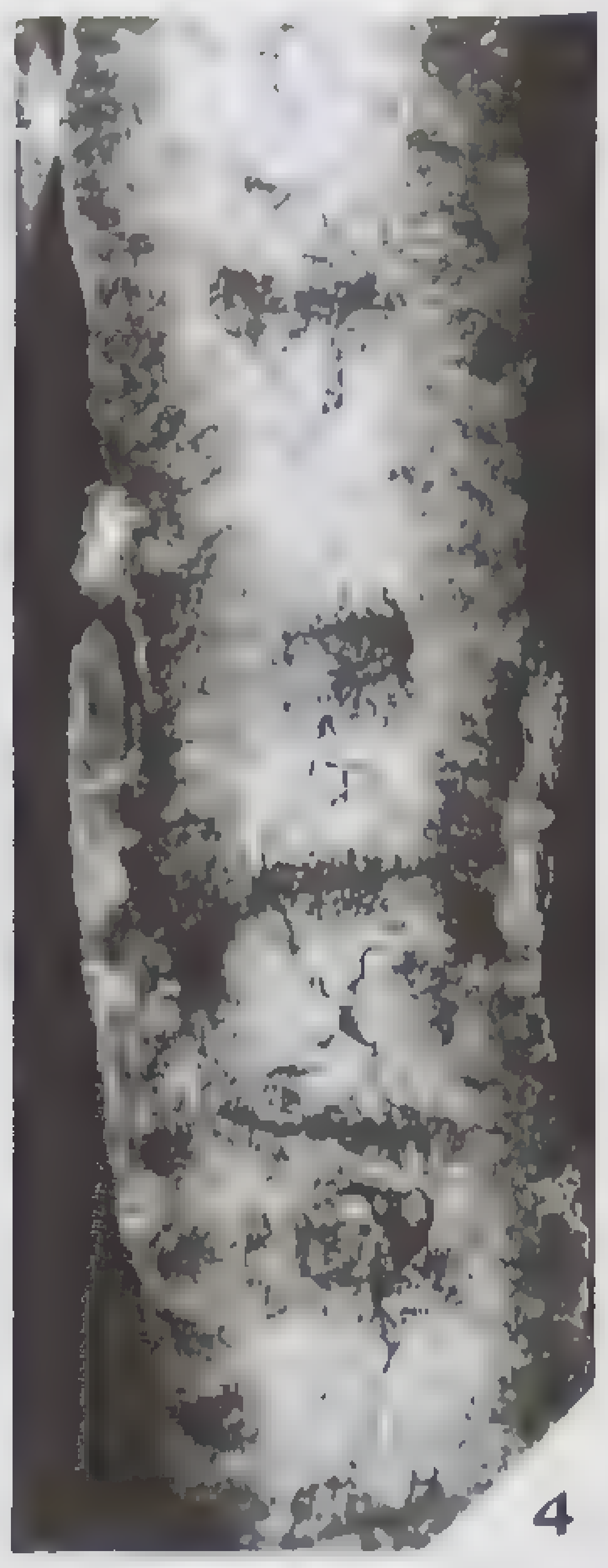
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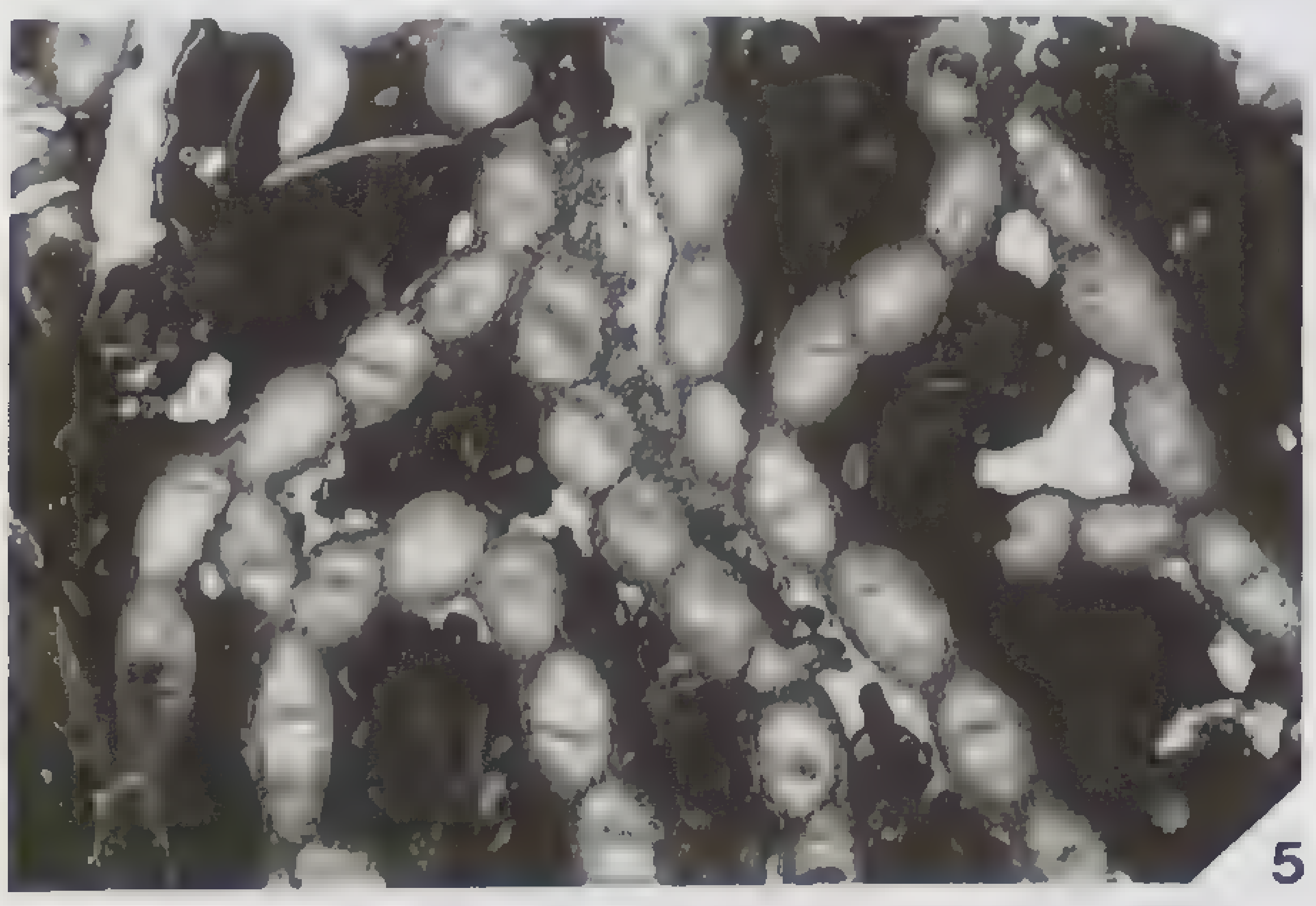
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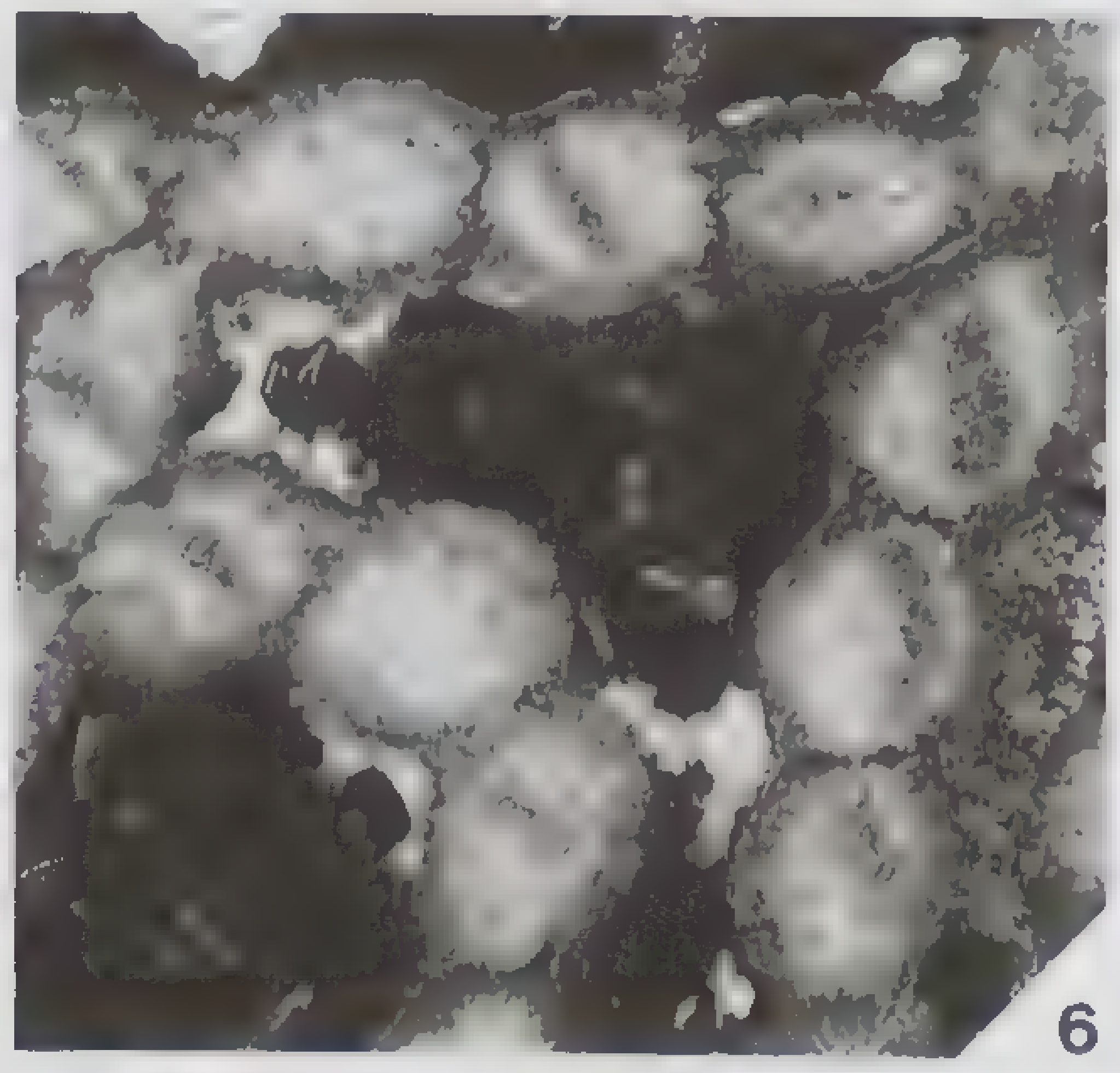
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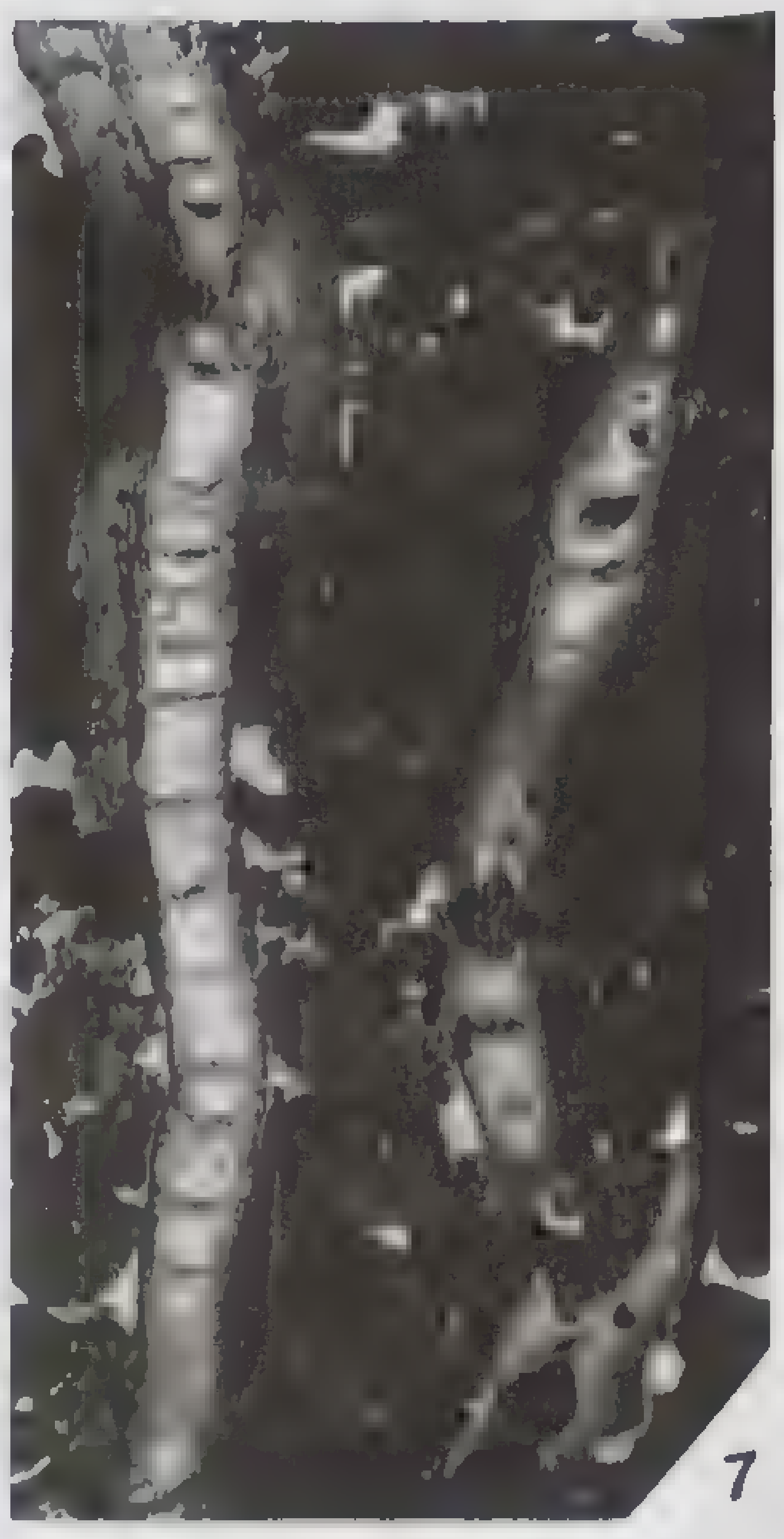
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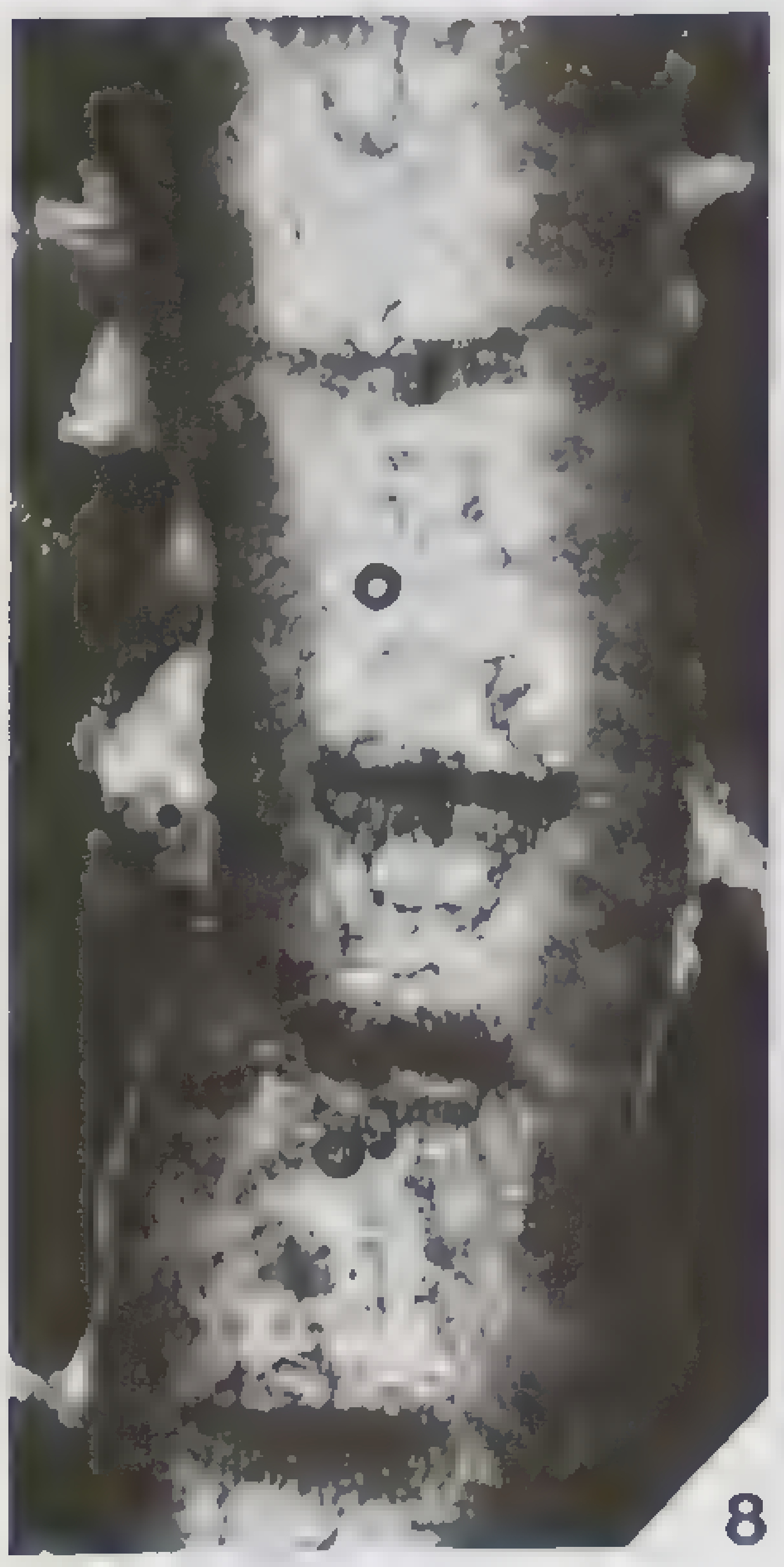
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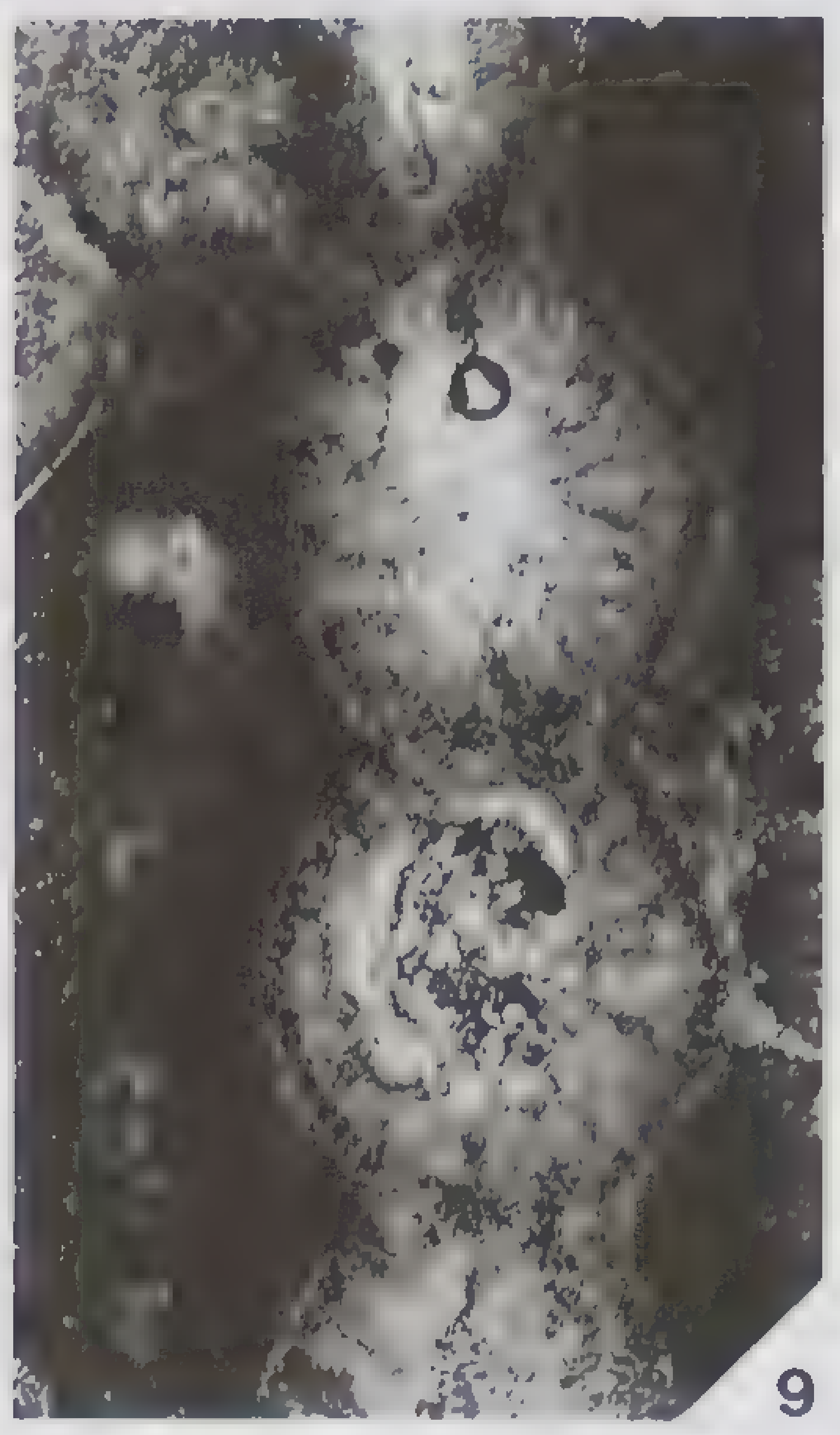
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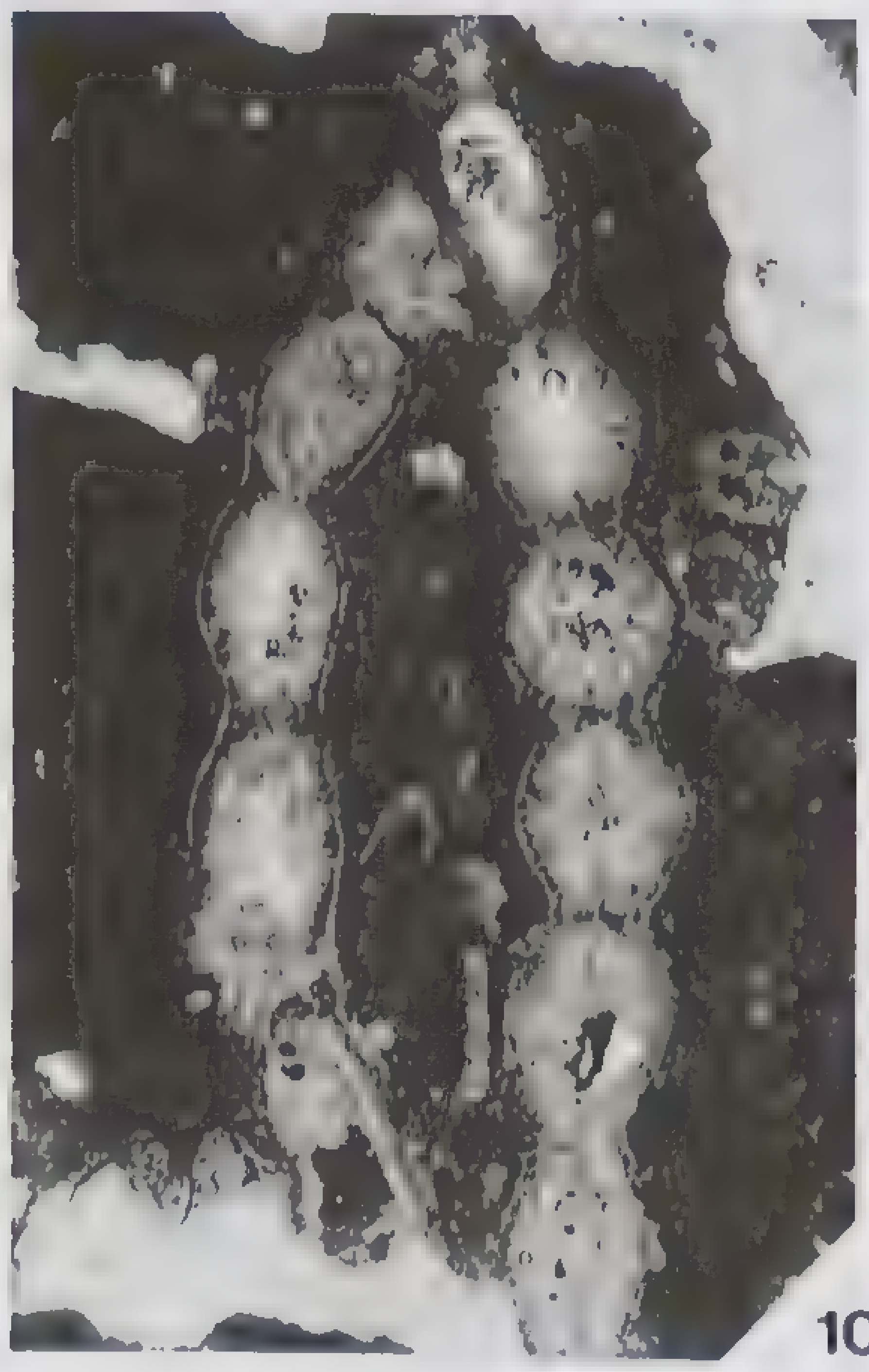
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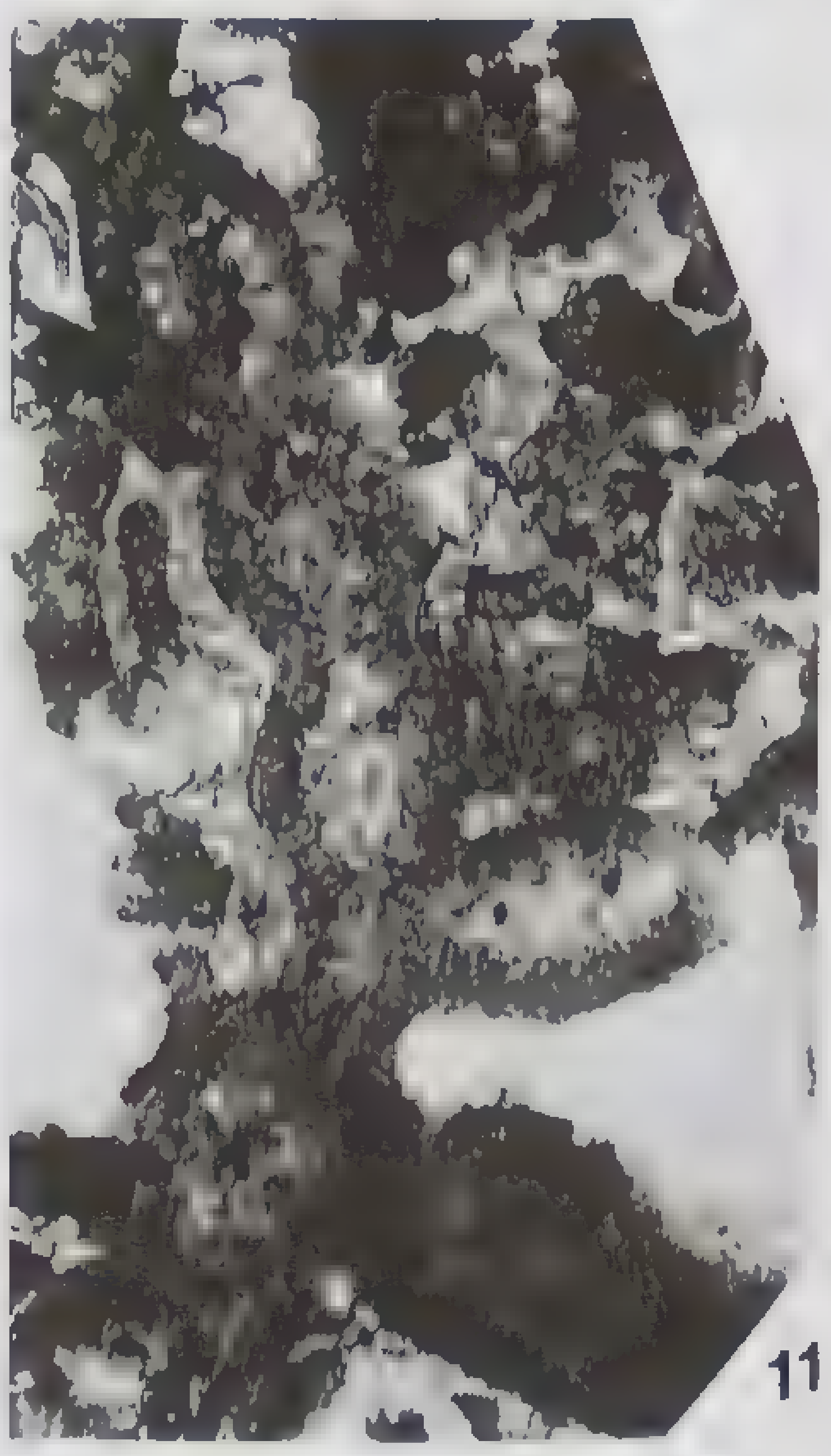
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EXPLANATION OF PLATE 12

Figure		Page
1, 2.	***Halysites*? species A**	73
	[1, 2, Sexton Creek Limestone, Sexton Creek, Illinois.]	
	1, 2. UI C-1346b: 1, transverse section, ×8; 2, longitudinal section, ×8.	
3–11.	***Catenipora lawrencica*,** new species	74
	[3–10, *Brevilamnulella* beds, Keel Formation, Section-interval 23-2 (Lawrence Quarry) (site 23iv); 11, Kissenger Limestone Member, Bryant Knob Formation, Section-interval 14-1 (Higginbotham Farm).]	
	3–6. USNM 485780b (holotype): 3, longitudinal section, ×8; 4, longitudinal section through a single corallite, showing rejuvenation (detail from upper left in 3, turned 10° clockwise), ×40; 5, transverse section, ×8; 6, transverse section (detail from left of center in 5, turned 40° clockwise), ×15.	
	7–10. USNM 485785c (paratype): 7, longitudinal section, ×8; 8, longitudinal section (detail from lower left of center in 7), ×40; 9, transverse section (detail from upper right of center in 10), ×40; 10, transverse section, ×15.	
	11. USNM 485812b (paratype): transverse section, ×15.	

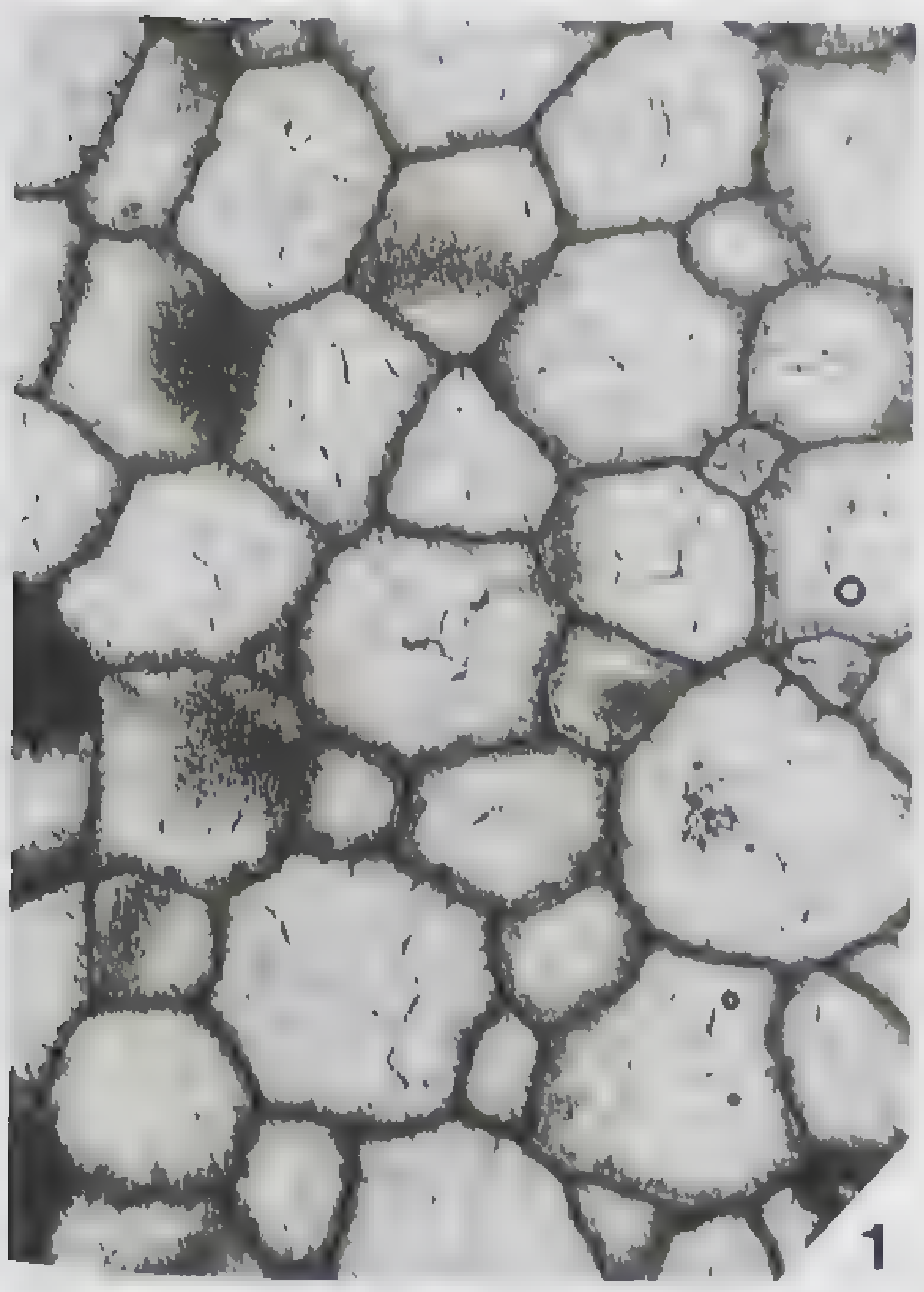
EXPLANATION OF PLATE 13

Figure Page

1–11. ***Paleofavosites subelongus*** (Savage, 1913) 78

[1, *Brevilamnulella* beds, Keel Formation, Section-interval 23-2 (Lawrence Quarry) (site 23iv); 2, 3, oölite of Keel Formation, Section-interval 23-3 (Lawrence Quarry) (site 23i); 4, 5, Leemon Formation, Section-interval 31-1 (Thebes North); 6, 7, unnamed member, Bryant Knob Formation, Section-interval 18-1 (Kissenger); 8–11, Bryant Knob Formation (undivided), 5 km south of Clarksville, Missouri.]

1. USNM 485785a: transverse section, ×8.
2, 3. USNM 458776: 2, longitudinal section, ×8; 3, transverse section, ×8.
4, 5. USNM 485819: 4, longitudinal section, ×8; 5, transverse section, ×8.
6, 7. USNM 485824: 6, transverse section, ×8; 7, longitudinal section, ×8.
8, 9. UI X-878a (holotype): 8, transverse section, ×8; 9, longitudinal section, ×8.
10, 11. UI C-1465a: 10, transverse section, ×8; 11, longitudinal section, ×8.



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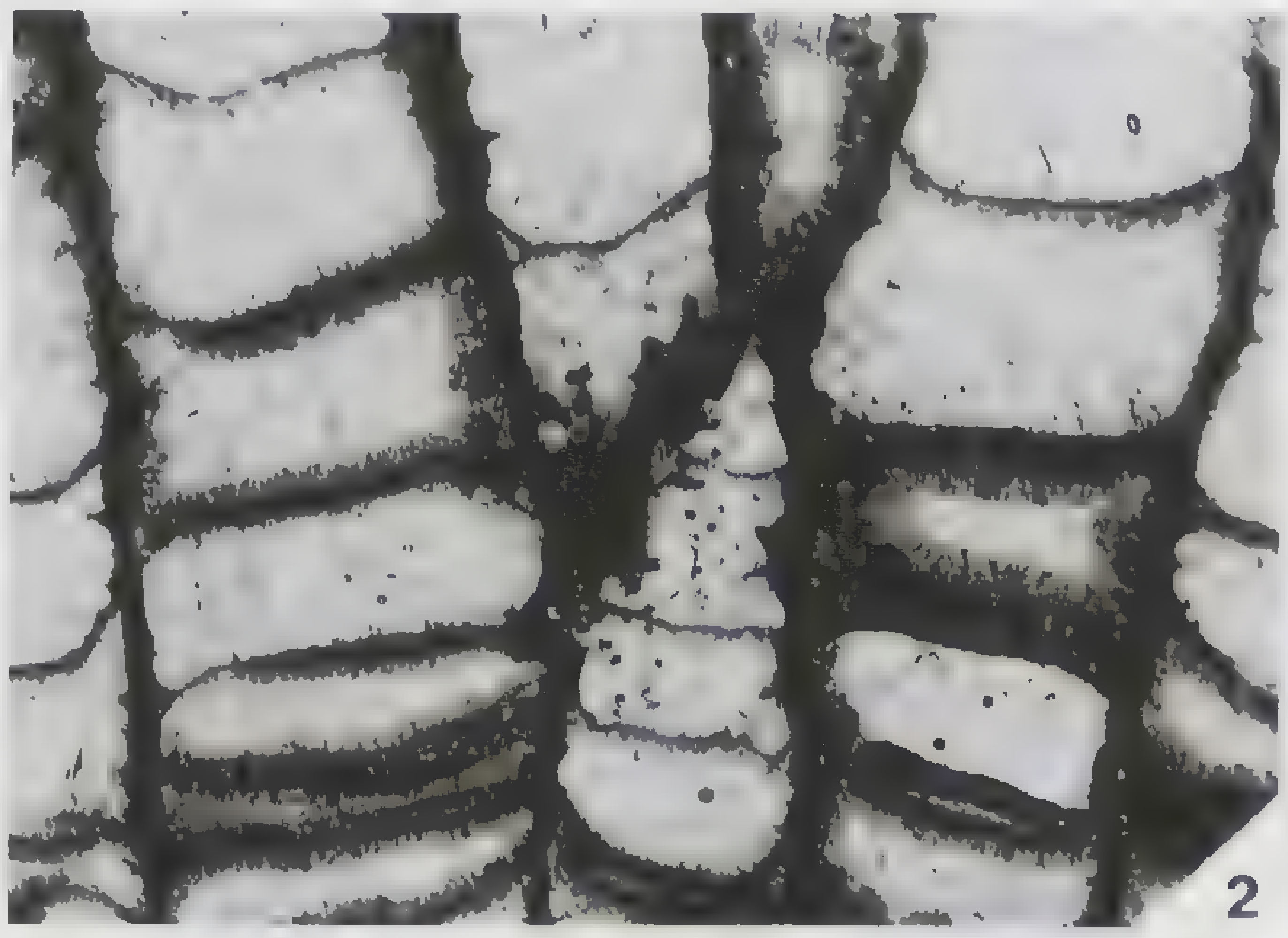

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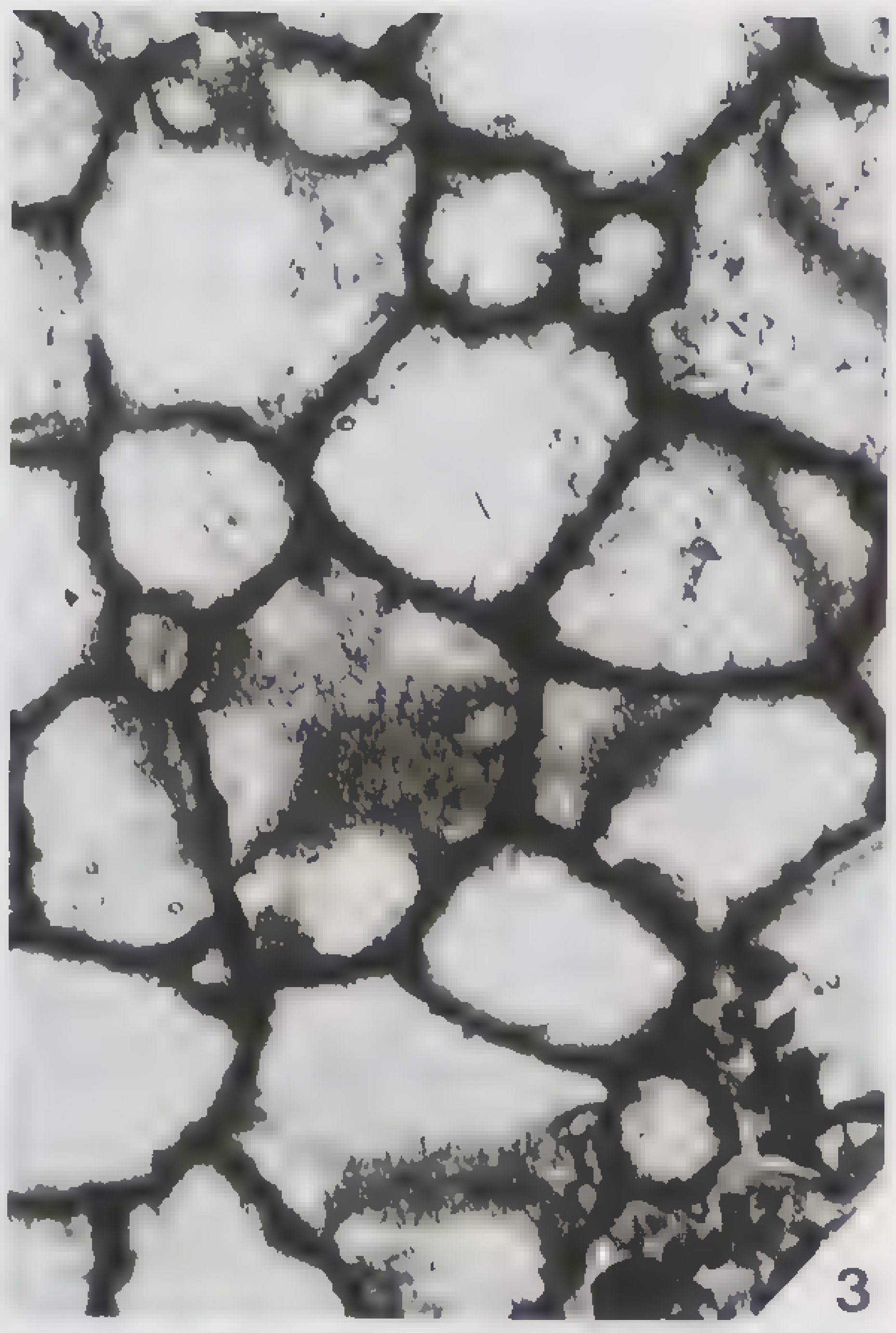

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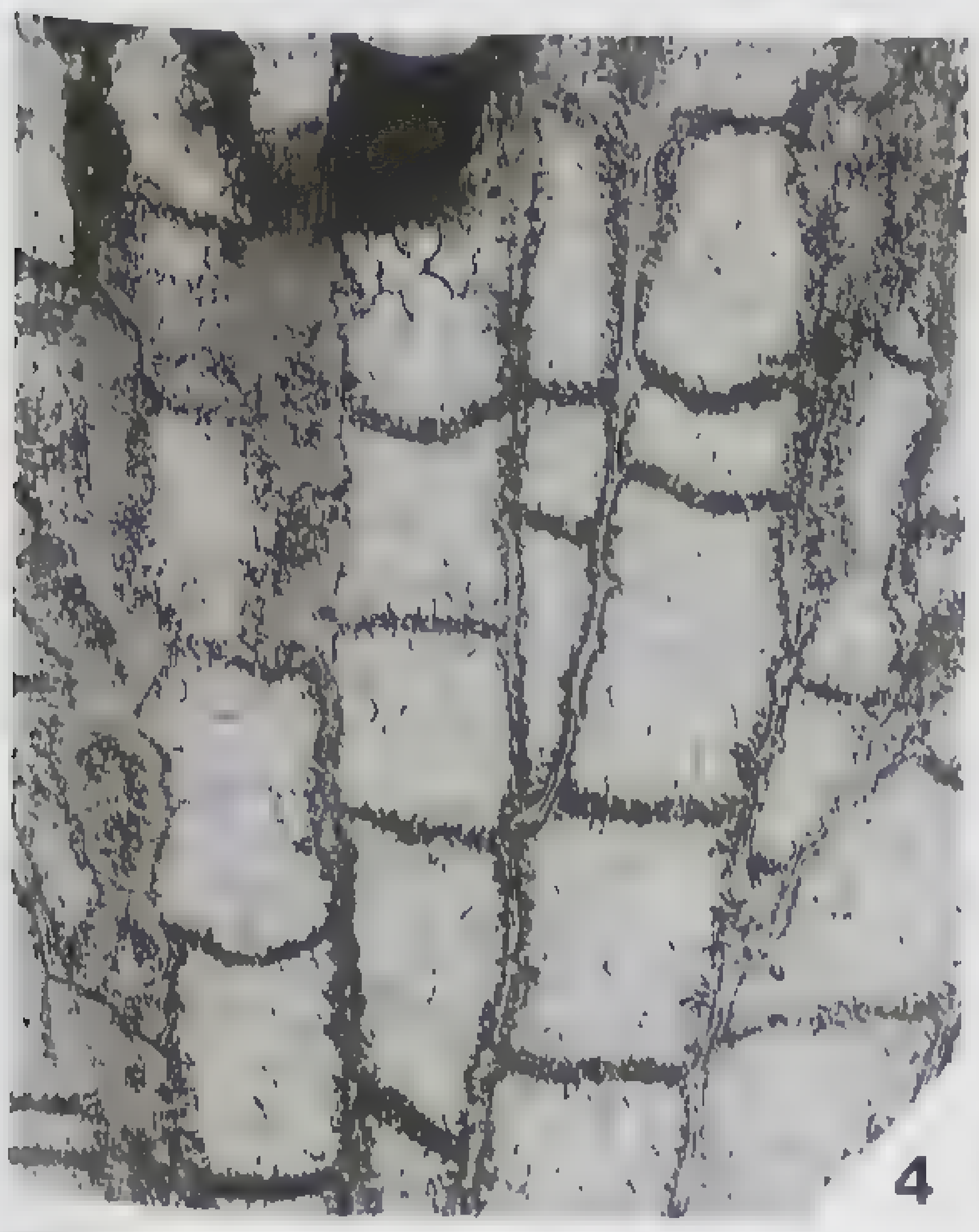

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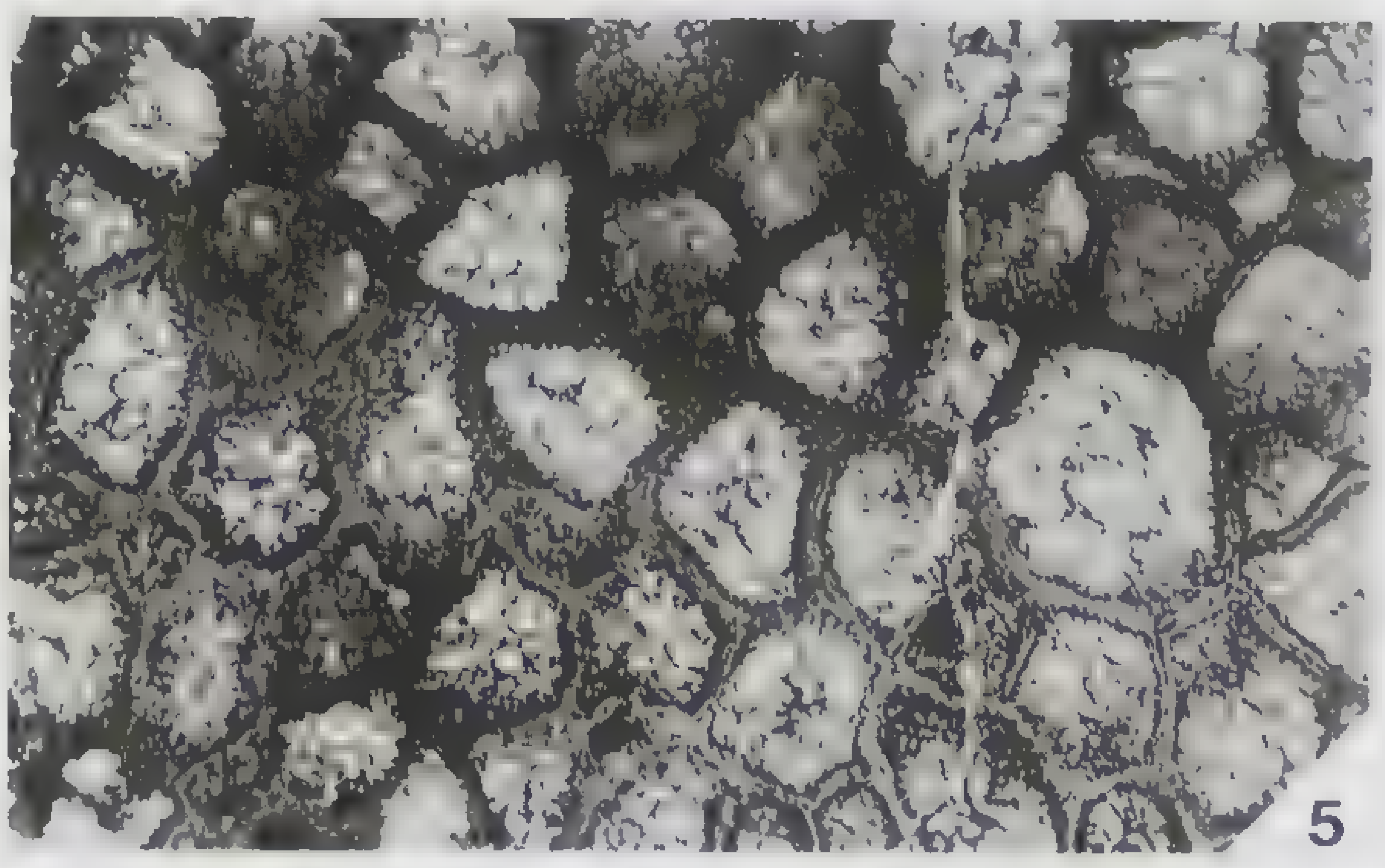

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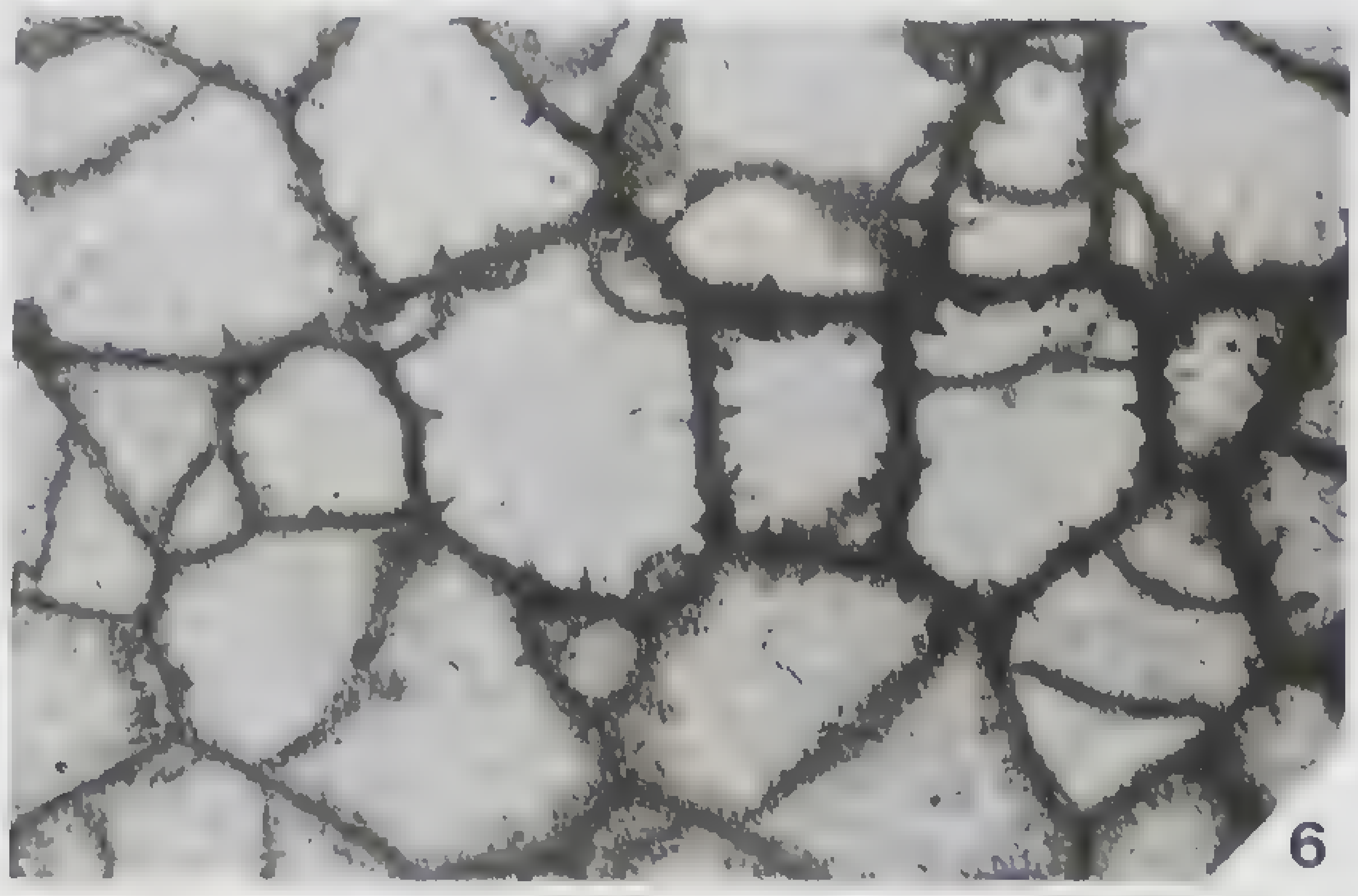

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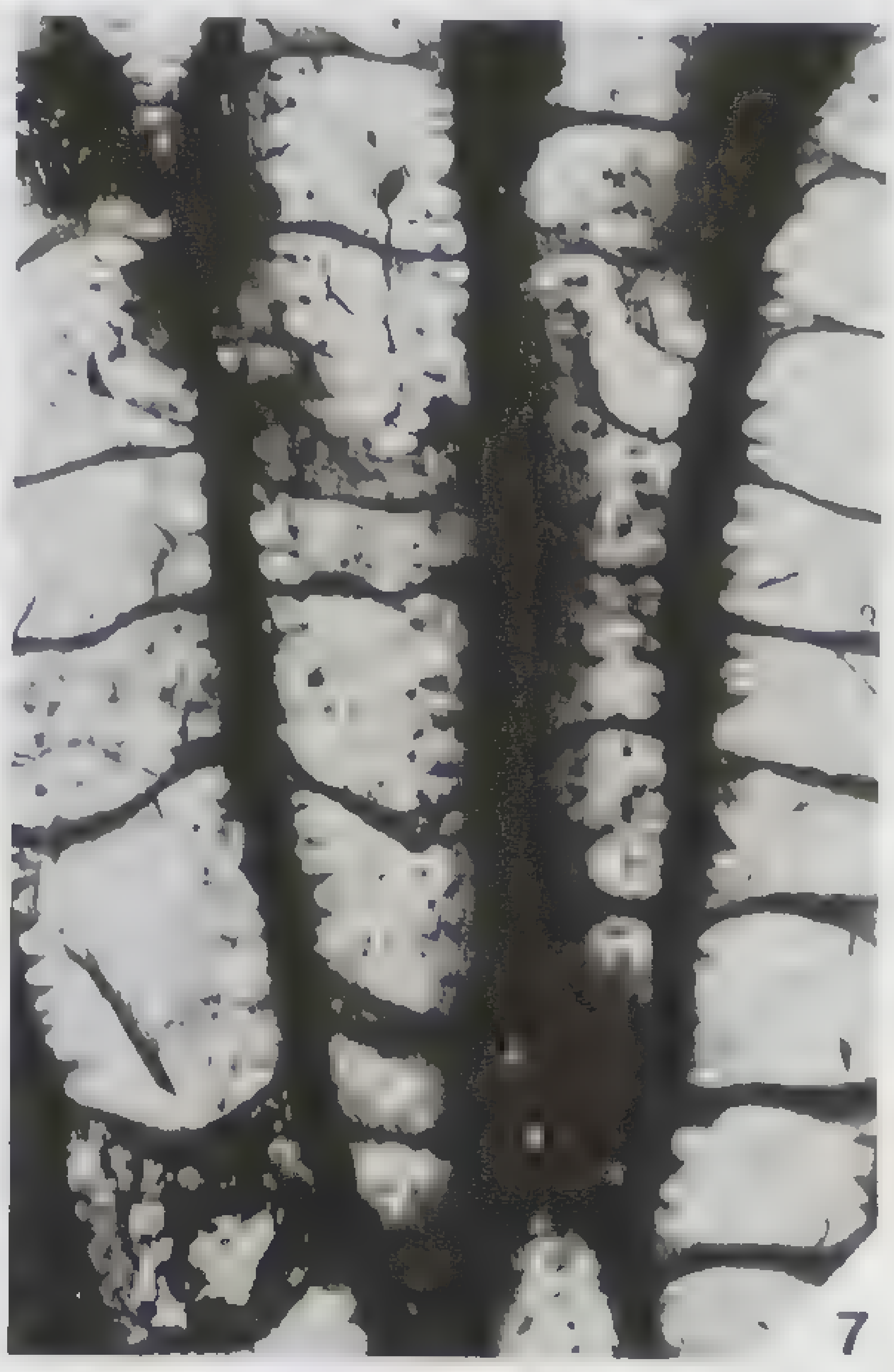

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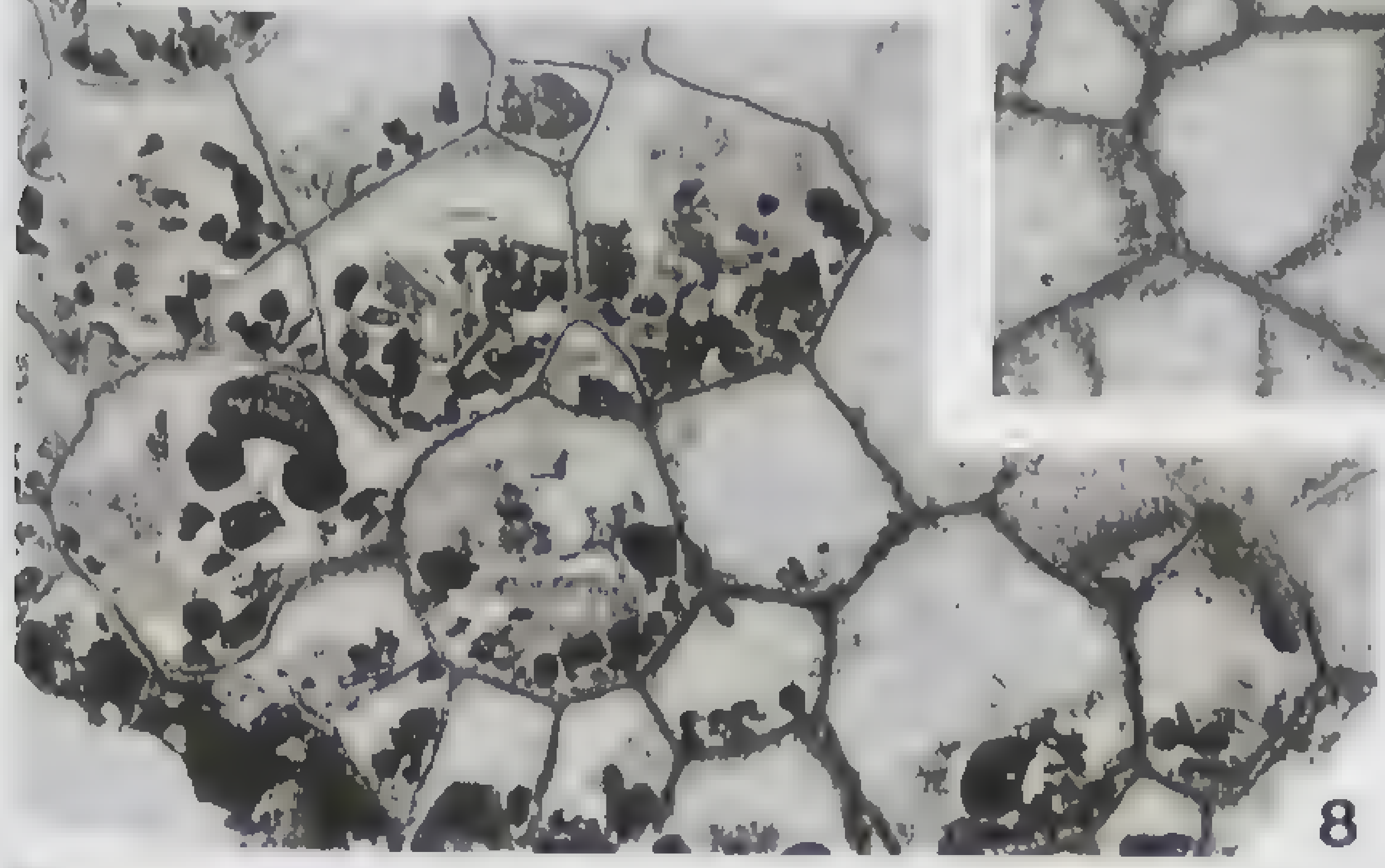

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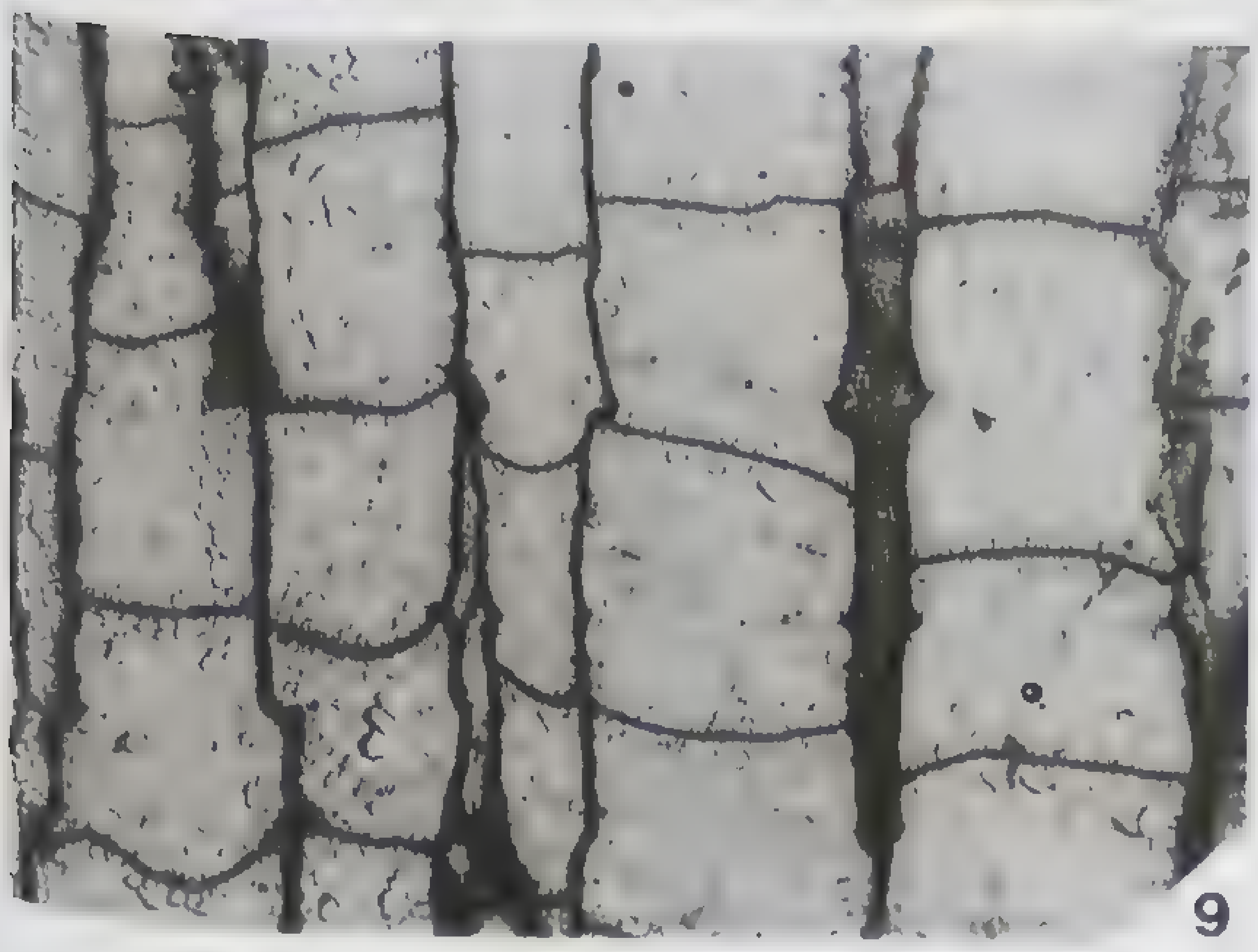

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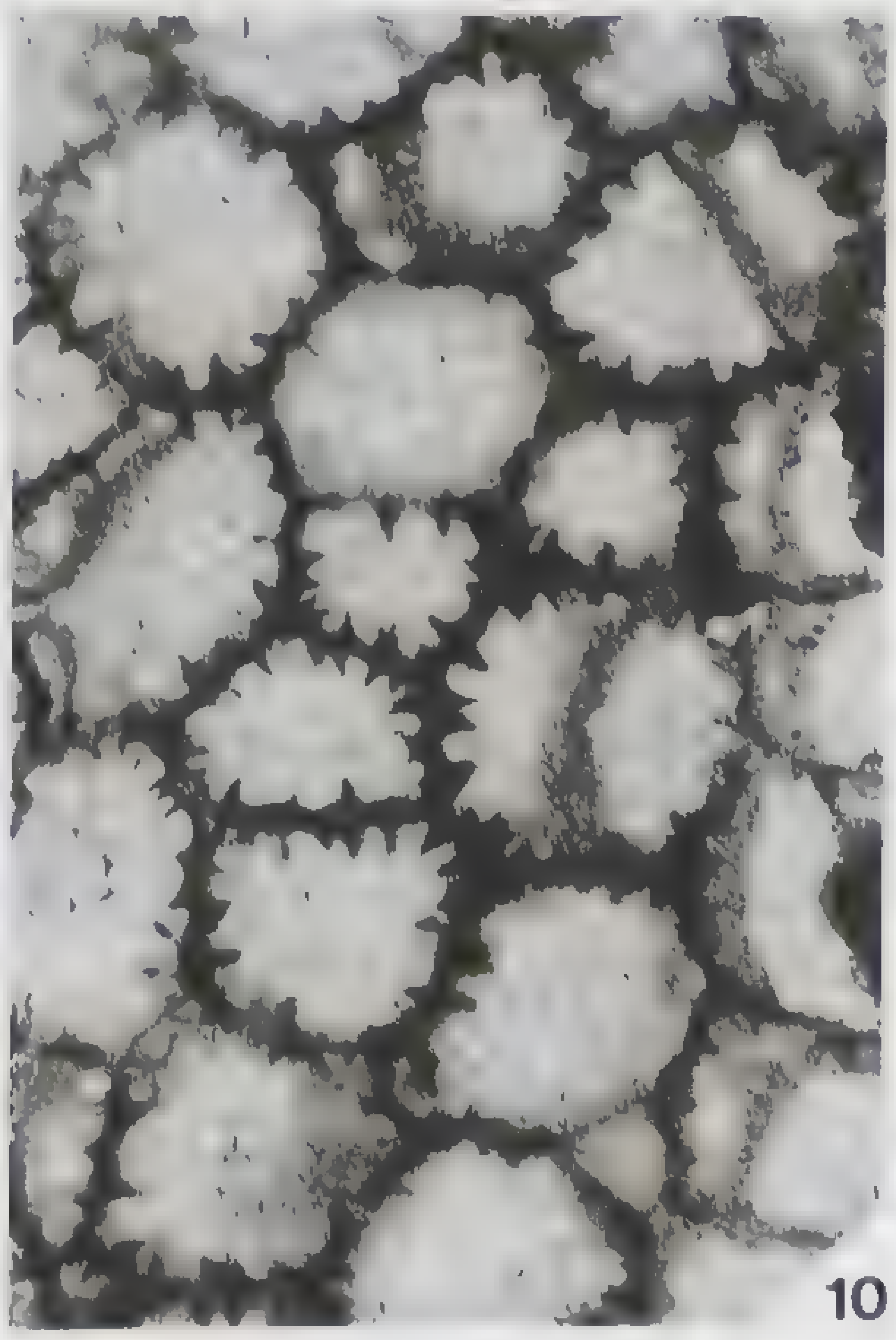

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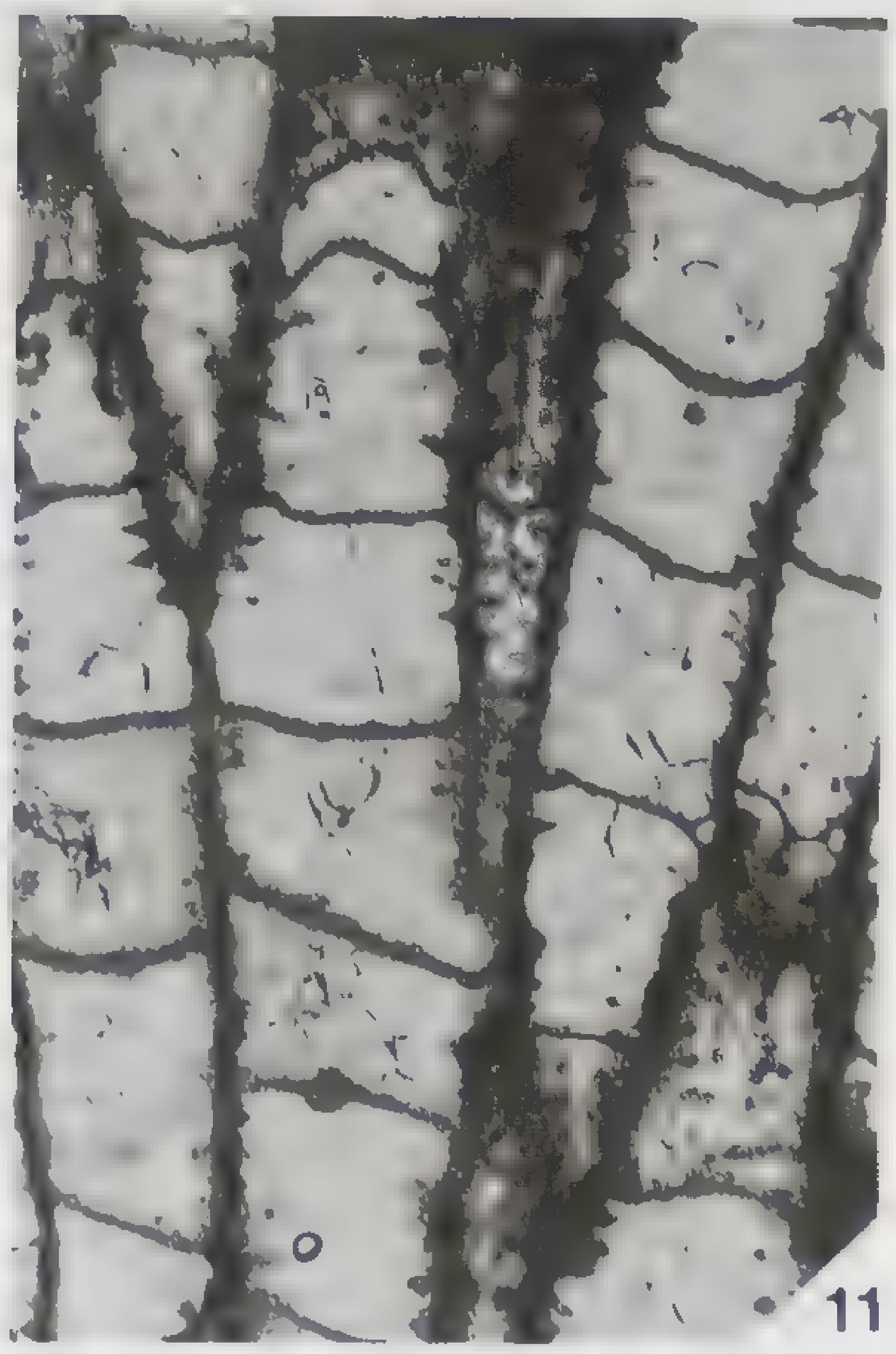

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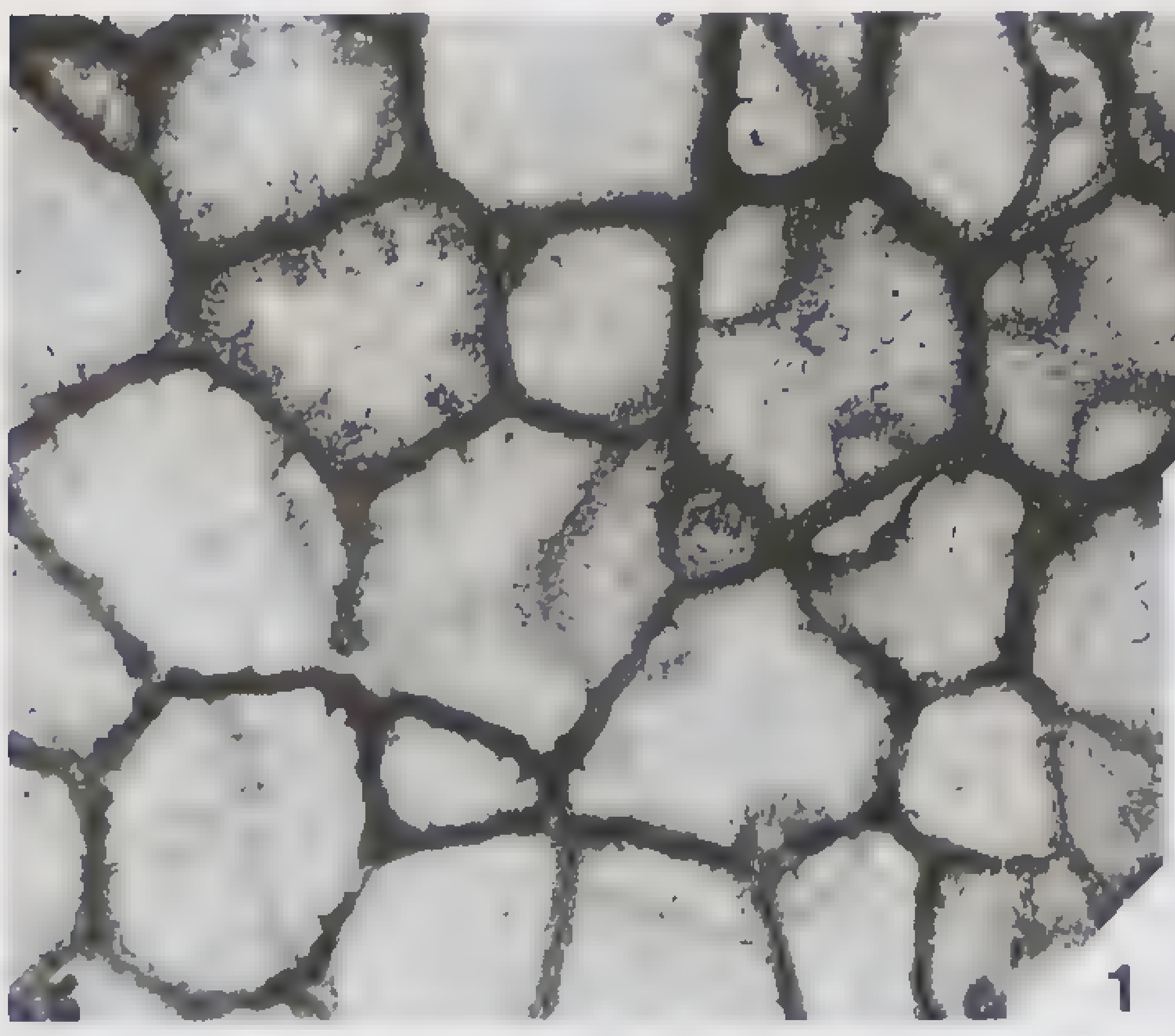
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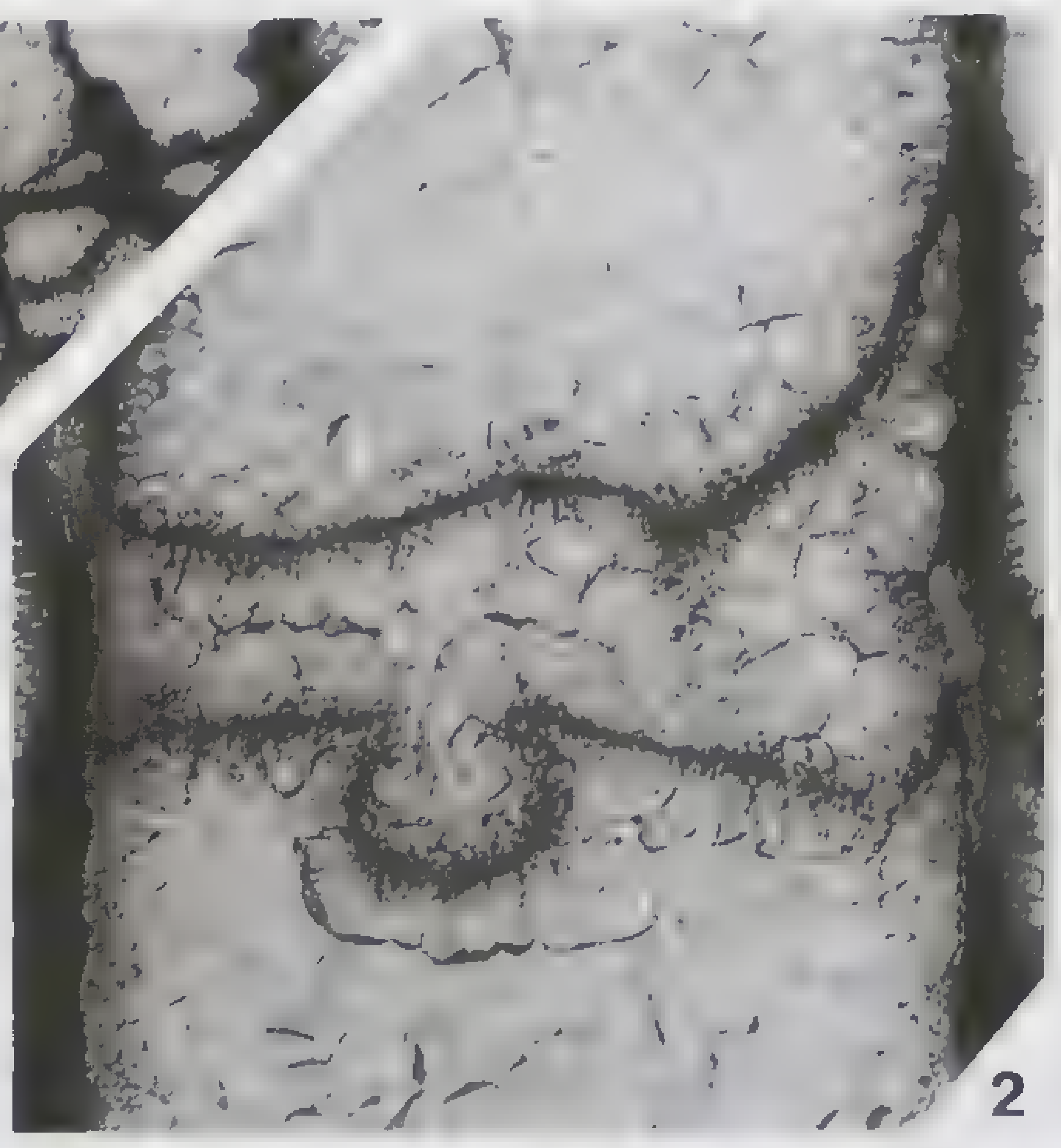
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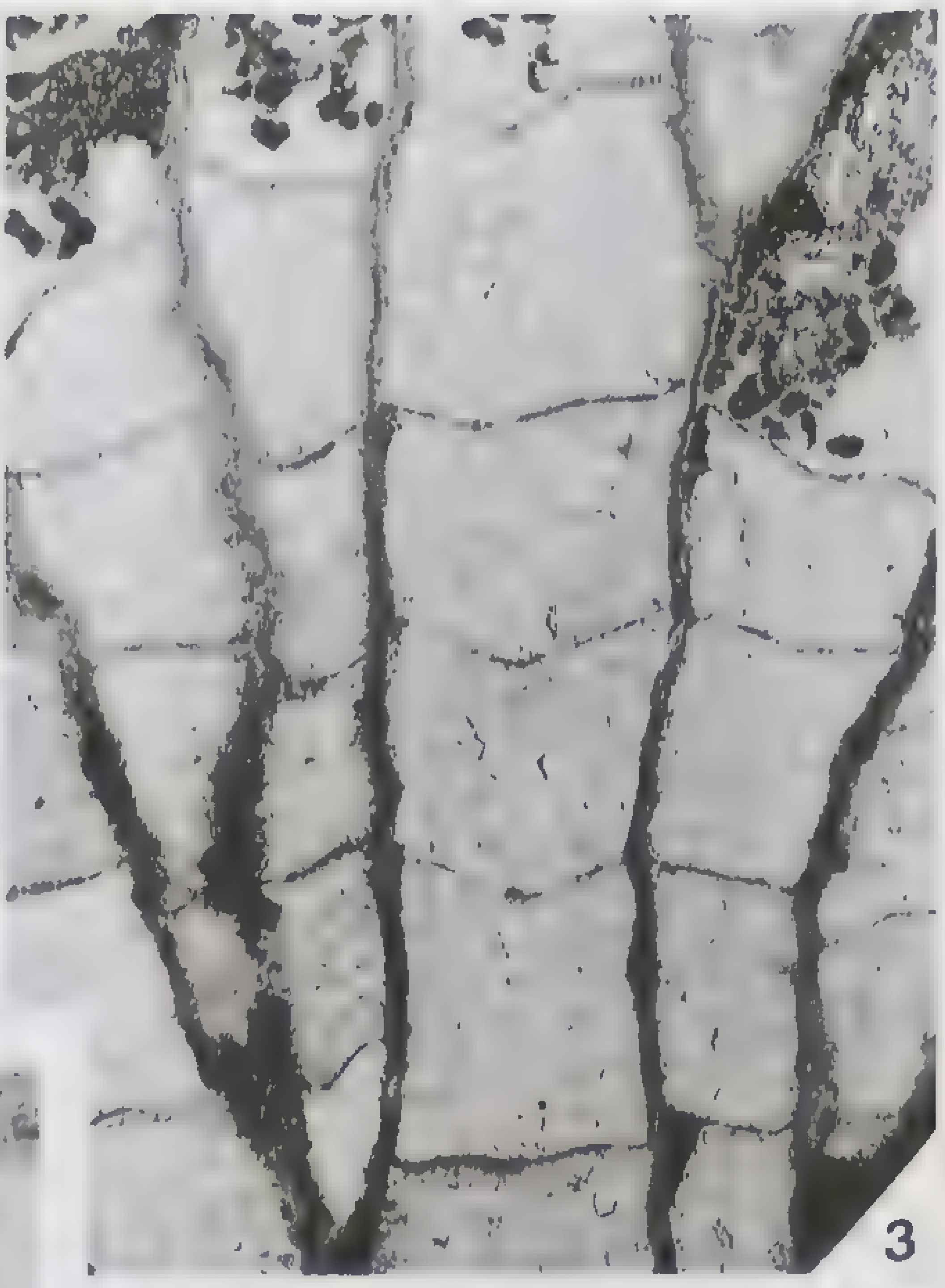
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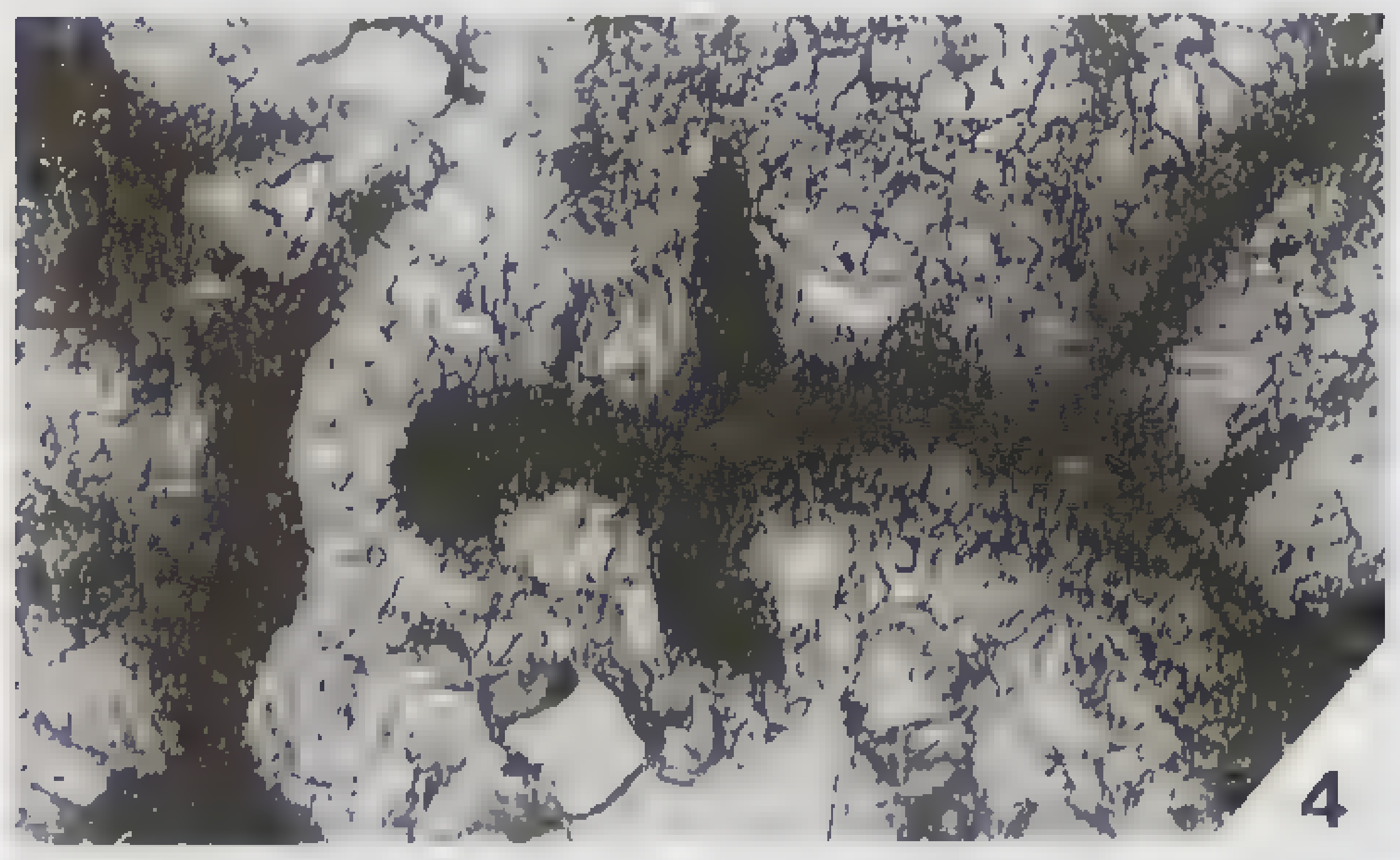
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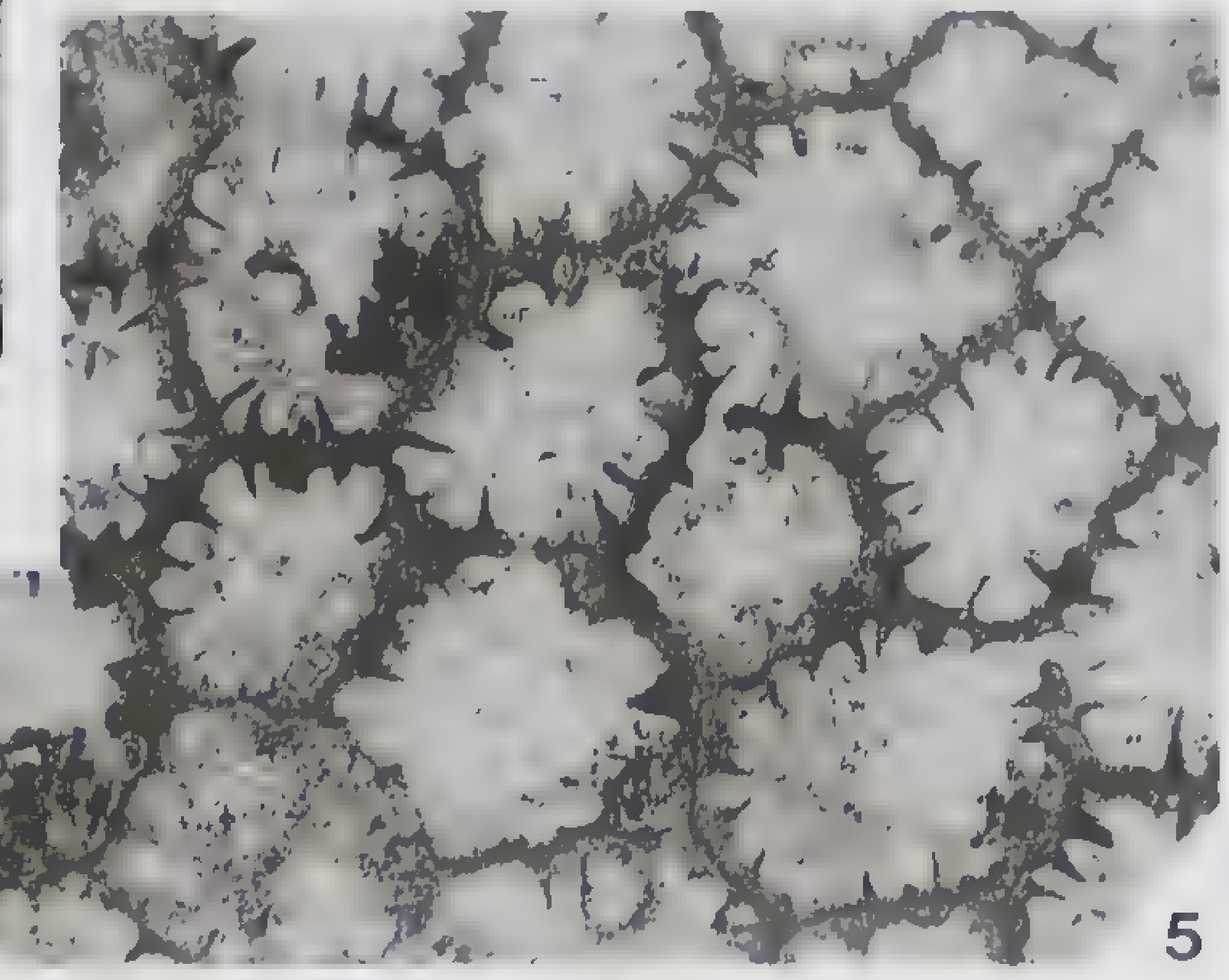
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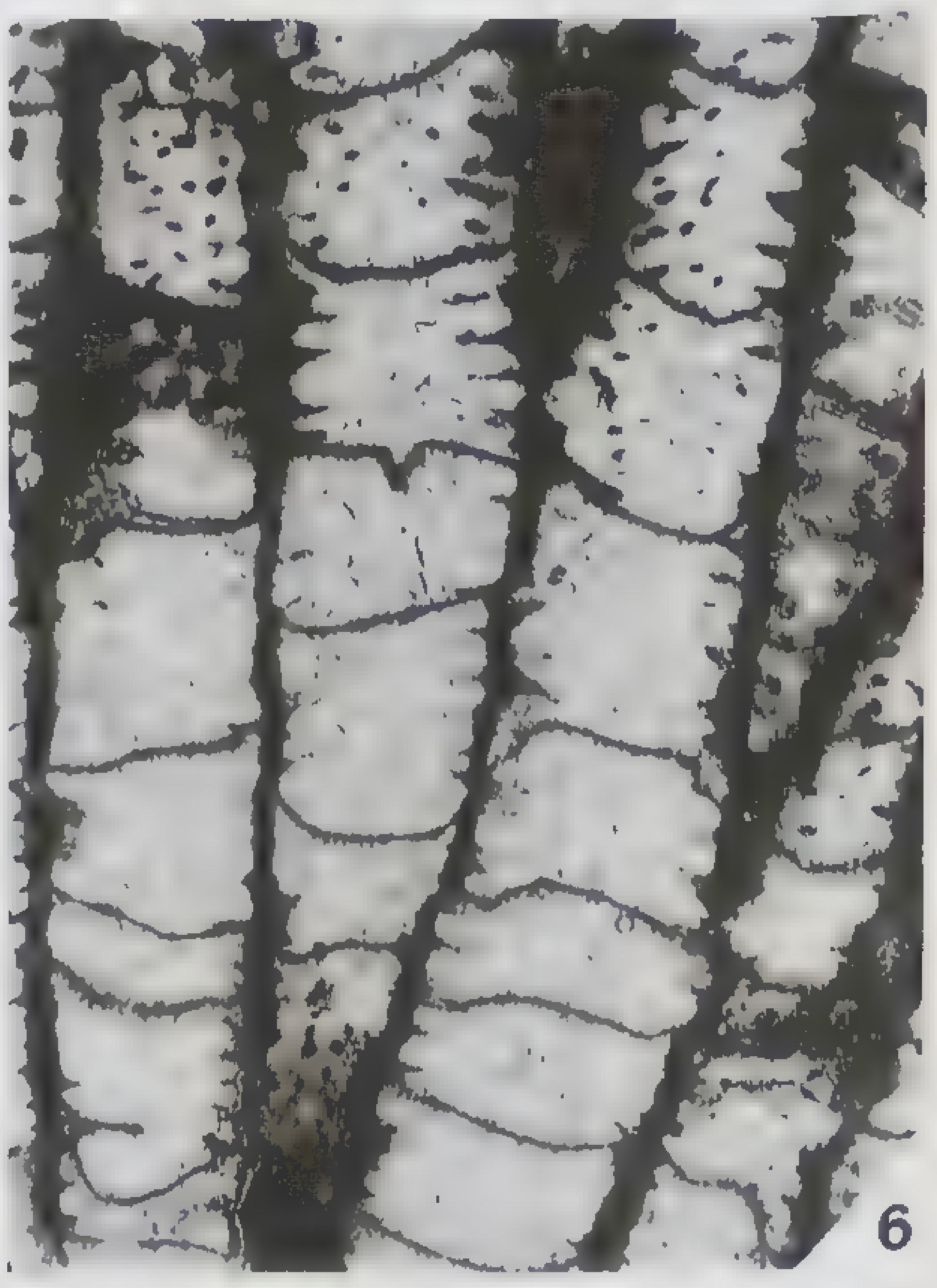
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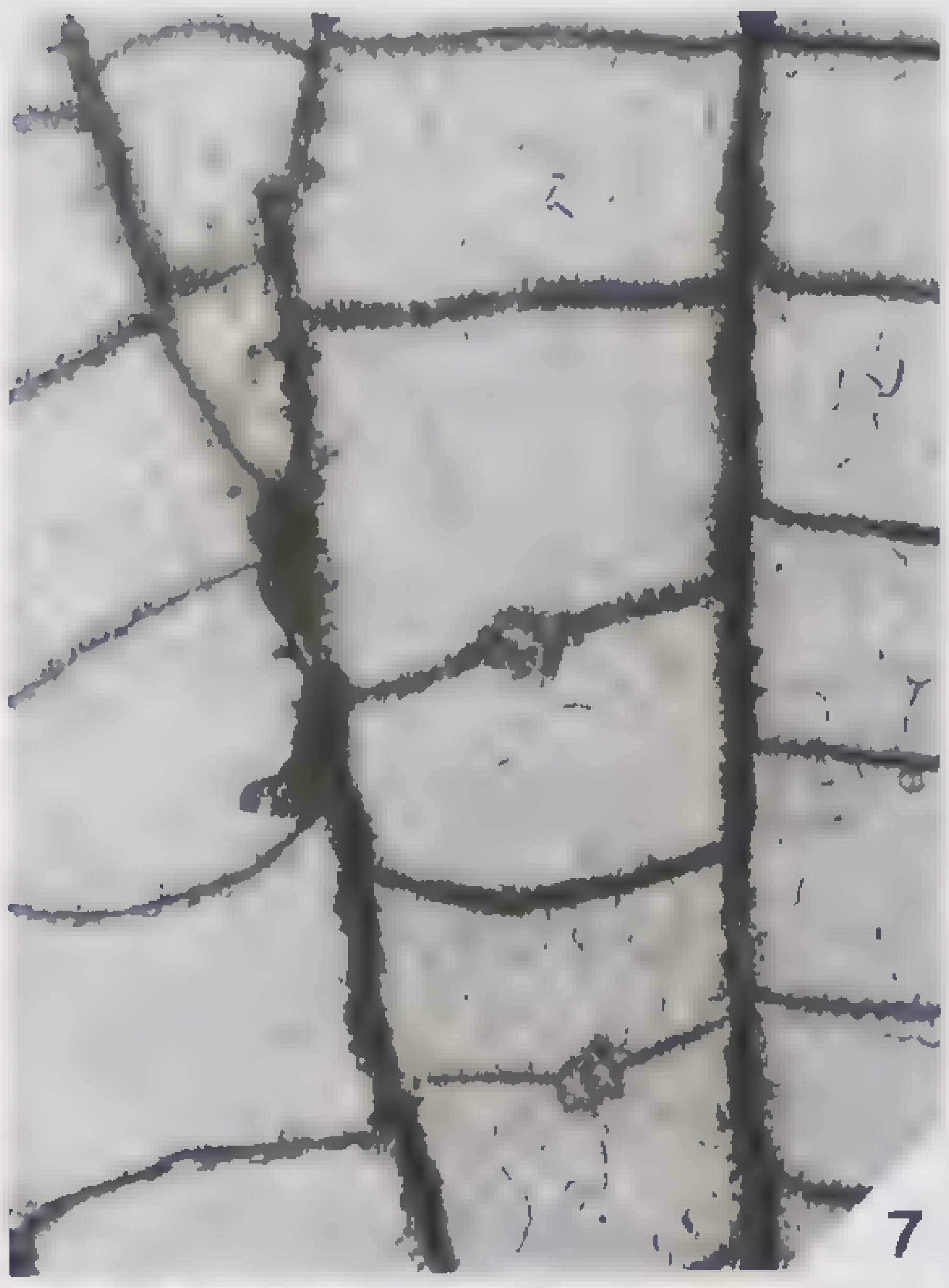
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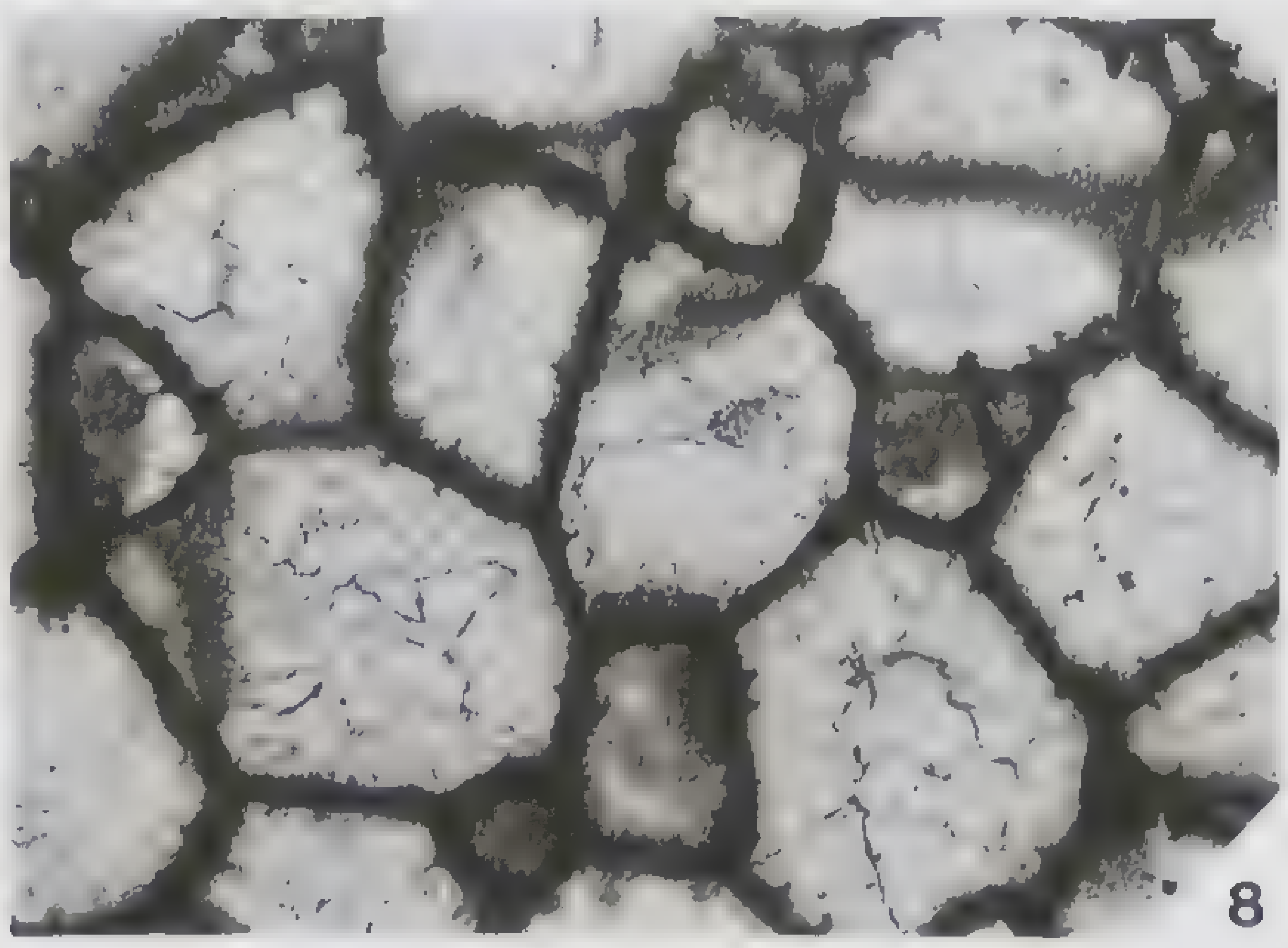
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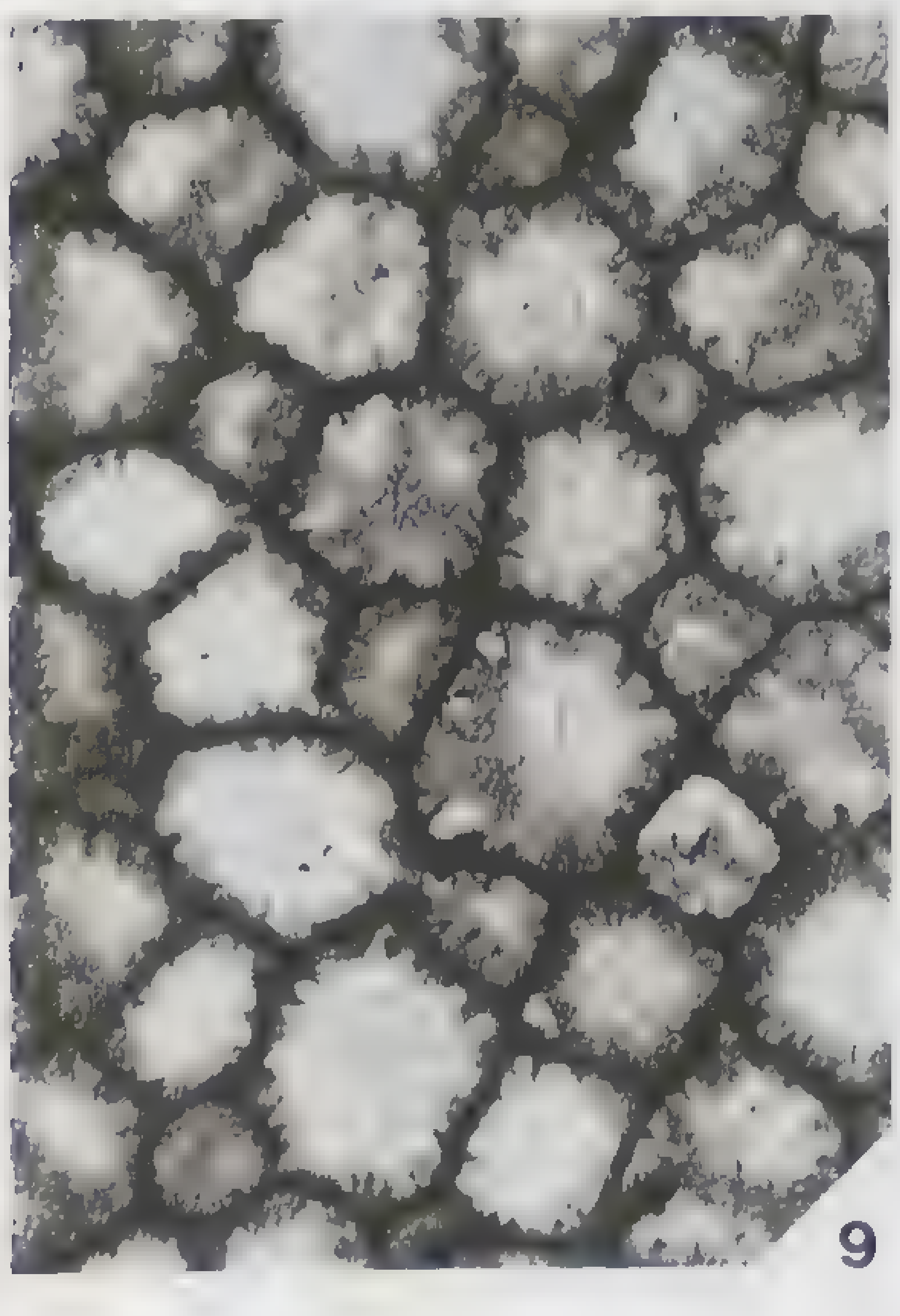
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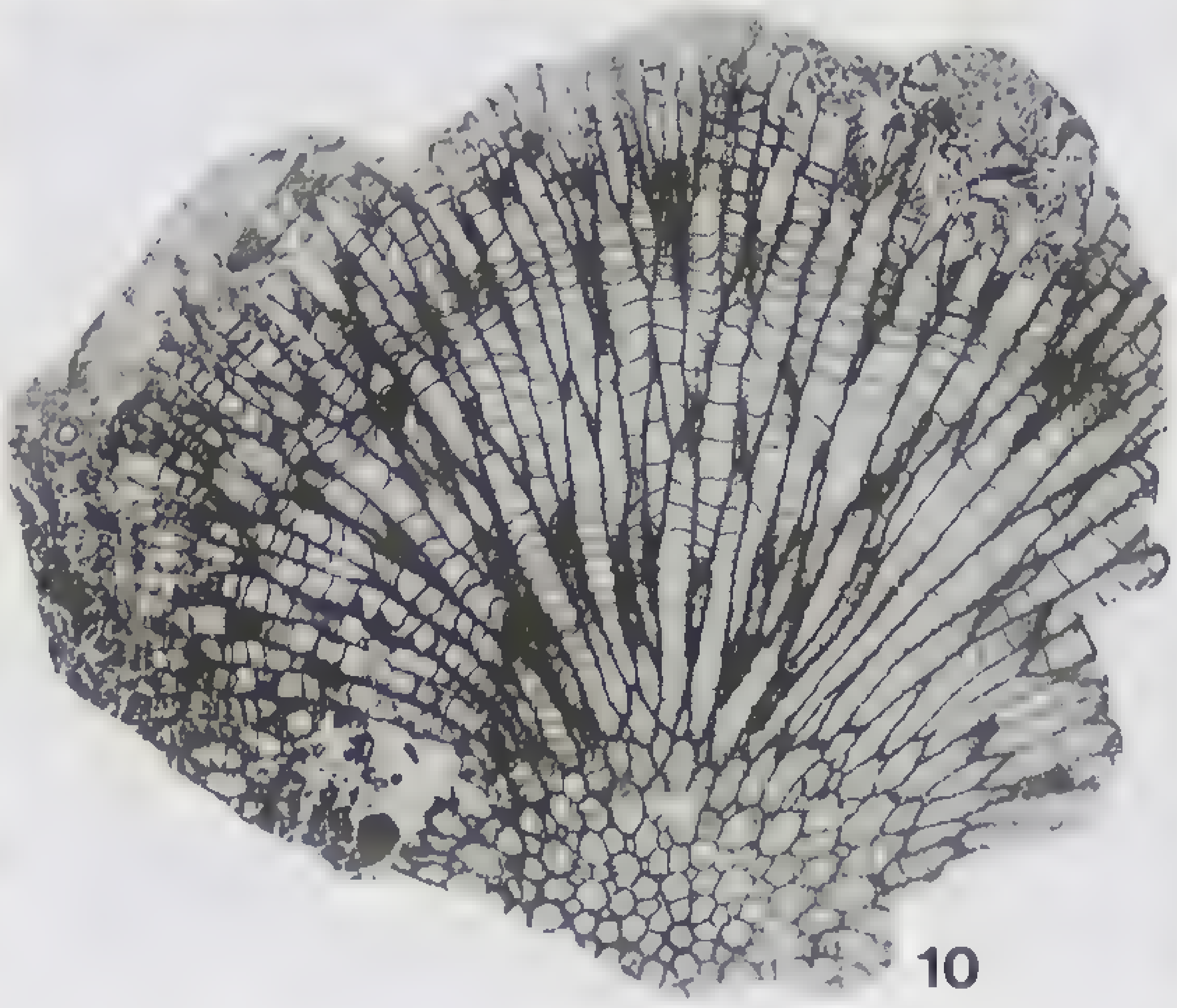
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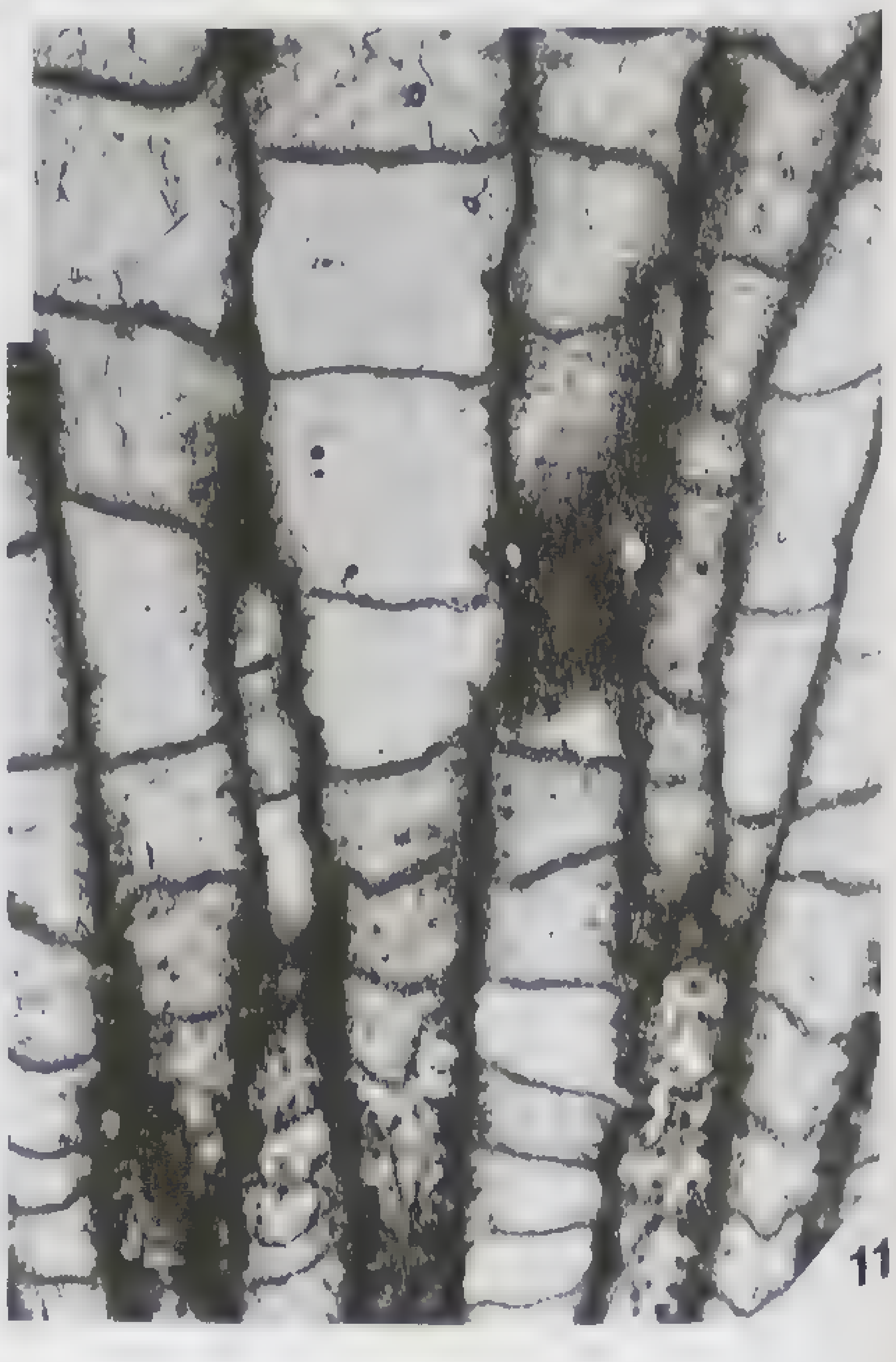
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EXPLANATION OF PLATE 14

Figure Page

1–11. ***Paleofavosites subelongus*** (Savage, 1913) 78

[1–3, Kissenger Limestone Member, Bryant Knob Formation, Section-interval 16-1 (Clinton Spring); 4–6, Bryant Knob Formation (undivided), Louisiana, Missouri; 7–11, Kissenger Limestone Member, Bryant Knob Formation, Section-interval 15-1 (Calumet).]

1–3. USNM 459086: 1, transverse section, ×8; 2, longitudinal section through a corallite, showing lobe-like depression in tabula, ×20; 3, longitudinal section, ×8.

4–6. UI X-771: 4, transverse section showing septa and corner pore (detail from right of center in 5, turned 10° counterclockwise), ×40; 5, transverse section, ×8; 6, longitudinal section, ×8.

7, 8. USNM 485834: 7, longitudinal section, ×8; 8, transverse section, ×8.

9–11. USNM 459074: 9, transverse section, ×8; 10, longitudinal section through entire corallum (note abrasion of upper surface), showing cyclomorphic variation and corallite expansion, ×1.5; 11, longitudinal section (detail from right of center in 10, turned 20° counterclockwise), ×8.

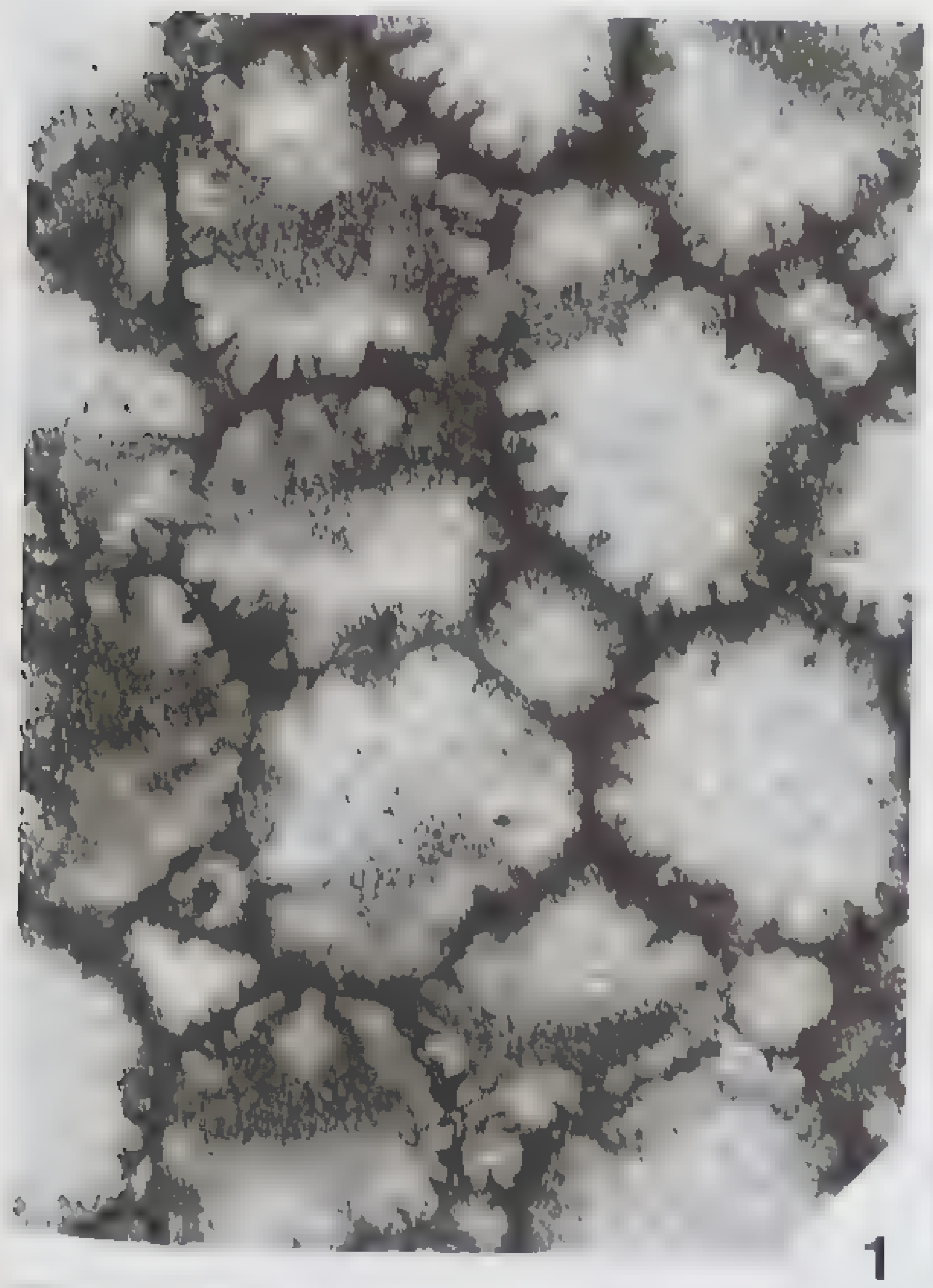
Explanation of Plate 15

Figure — Page

1–12. ***Paleofavosites subelongus*** (Savage, 1913) 78

[1, 2, Cyrene Formation, near Edgewood, Missouri; 3–12, Kissenger Limestone Member, Bryant Knob Formation, Section-interval 14-1 (Higginbotham Farm).]

1, 2. UI C-1458d: 1, transverse section, ×8; 2, longitudinal section, ×8.
3. USNM 485850: transverse section showing structure of walls and septa, ×40.
4. USNM 485848: longitudinal section showing structure of wall and septa, ×40.
5–7. USNM 459080: 5, longitudinal section, ×8; 6, longitudinal section showing regeneration, ×8; 7, transverse section, ×8.
8, 9. USNM 459078: 8, transverse section, ×8; 9, longitudinal section, ×8.
10–12. USNM 459081: 10, longitudinal section, ×8; 11, transverse section through upper part of corallum, ×8; 12, transverse section from lower in corallum, ×8.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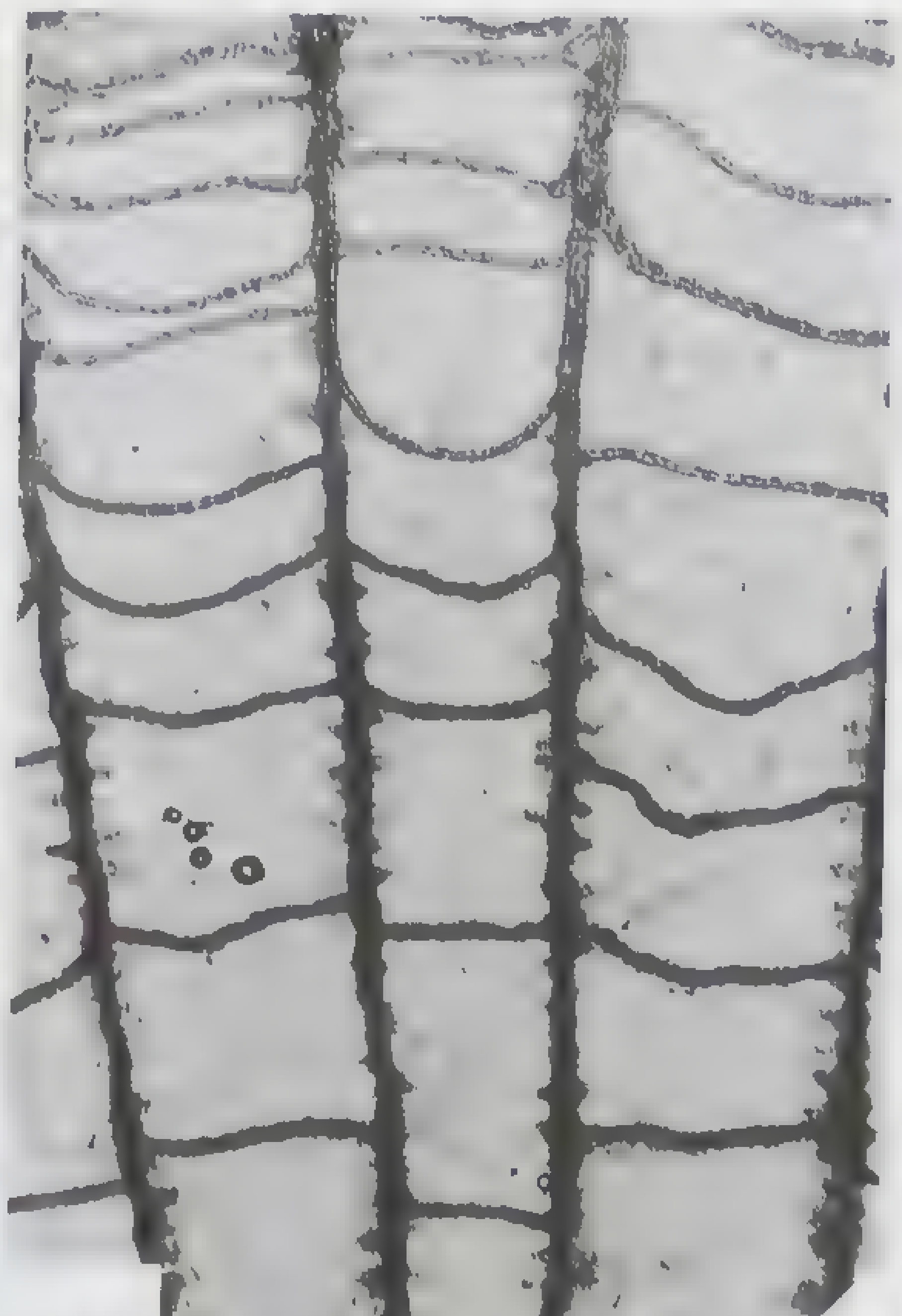
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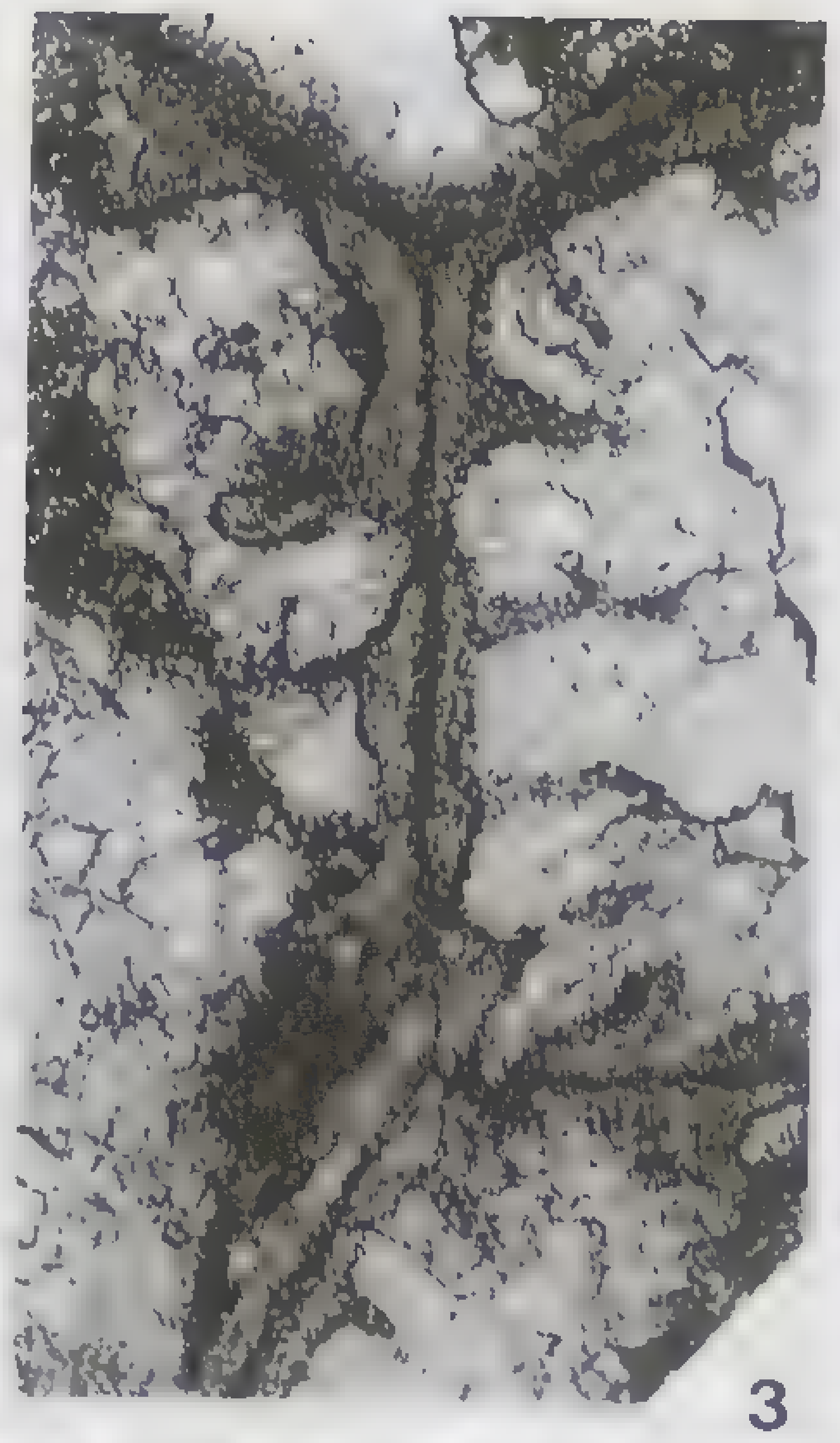
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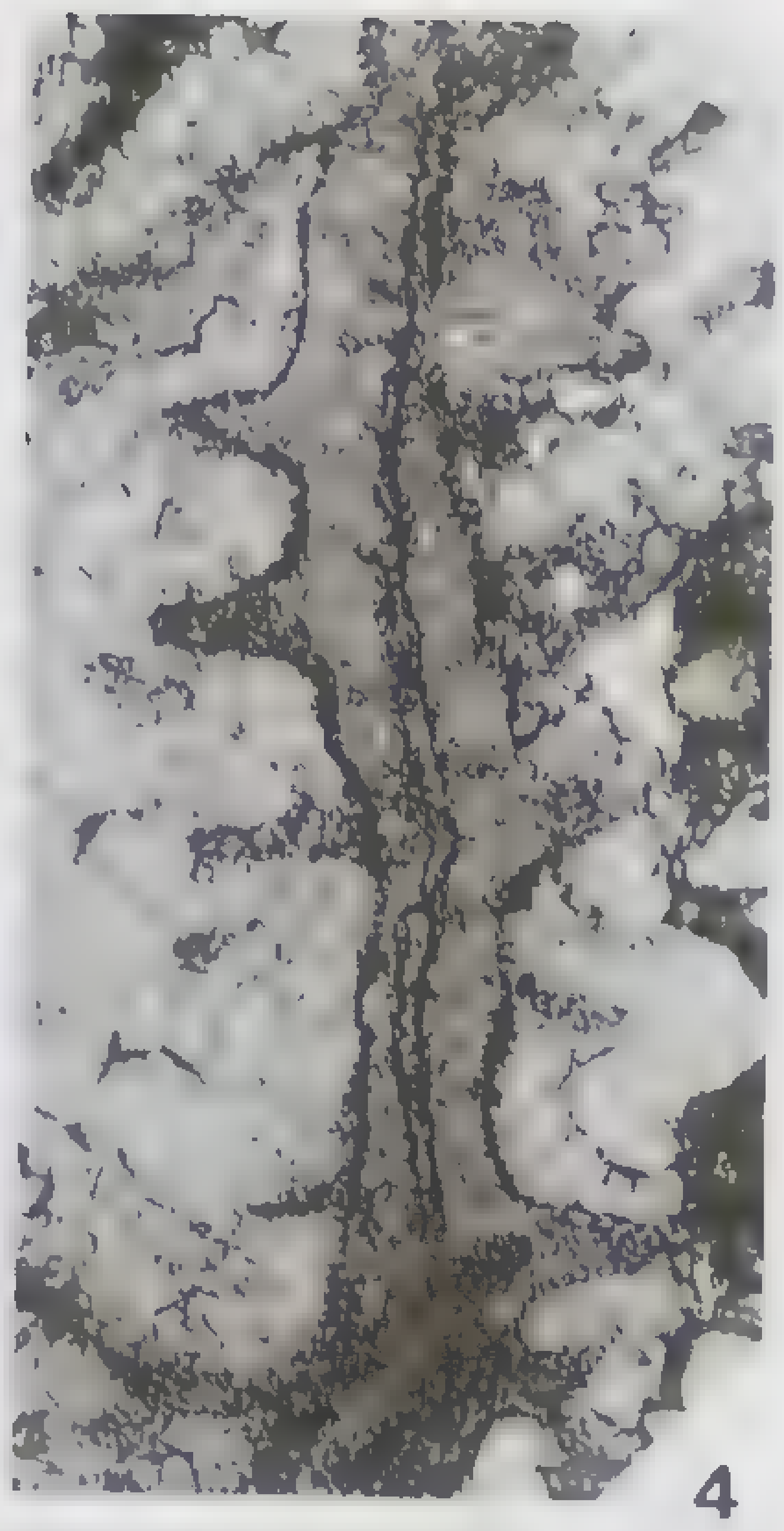
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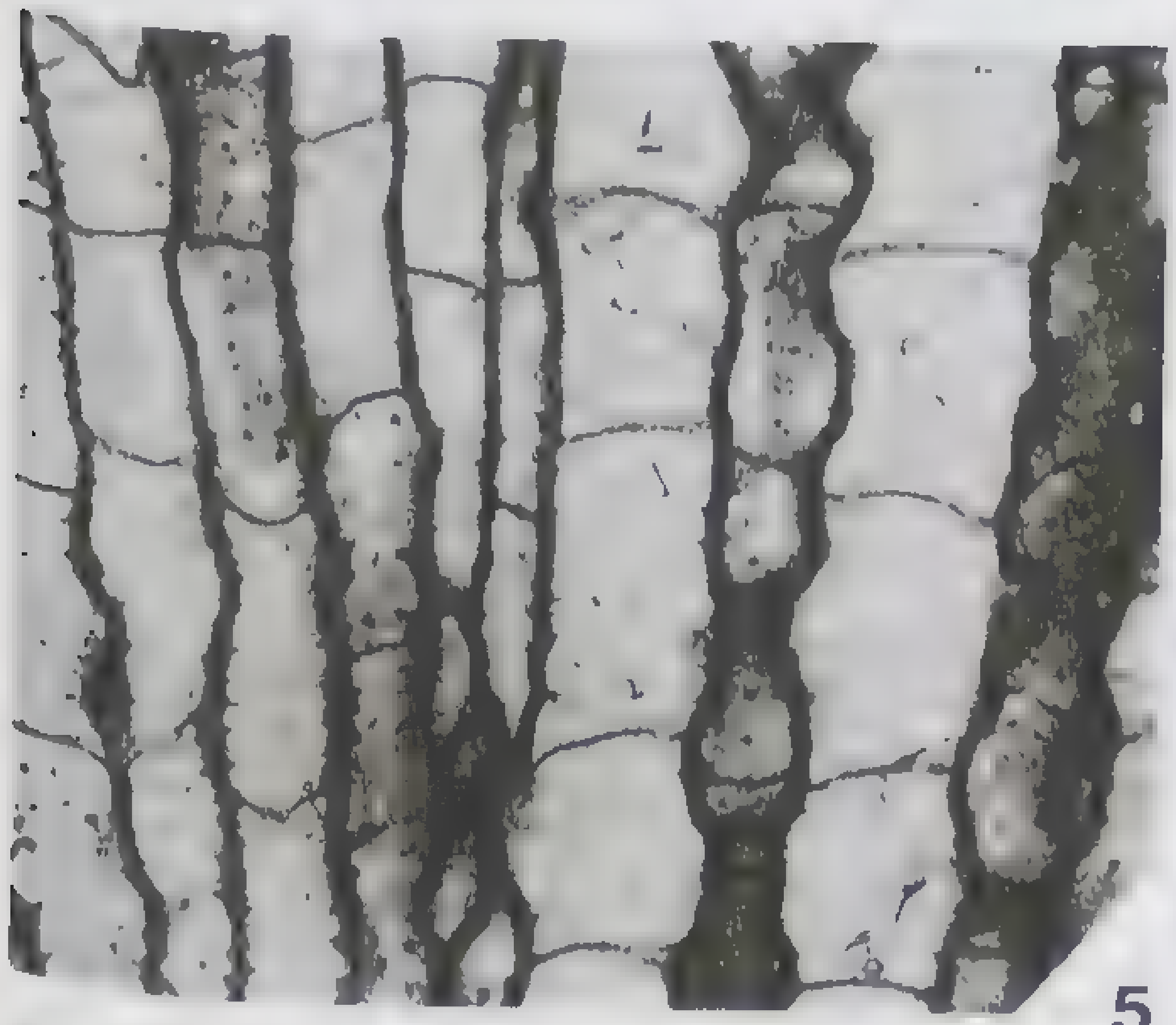
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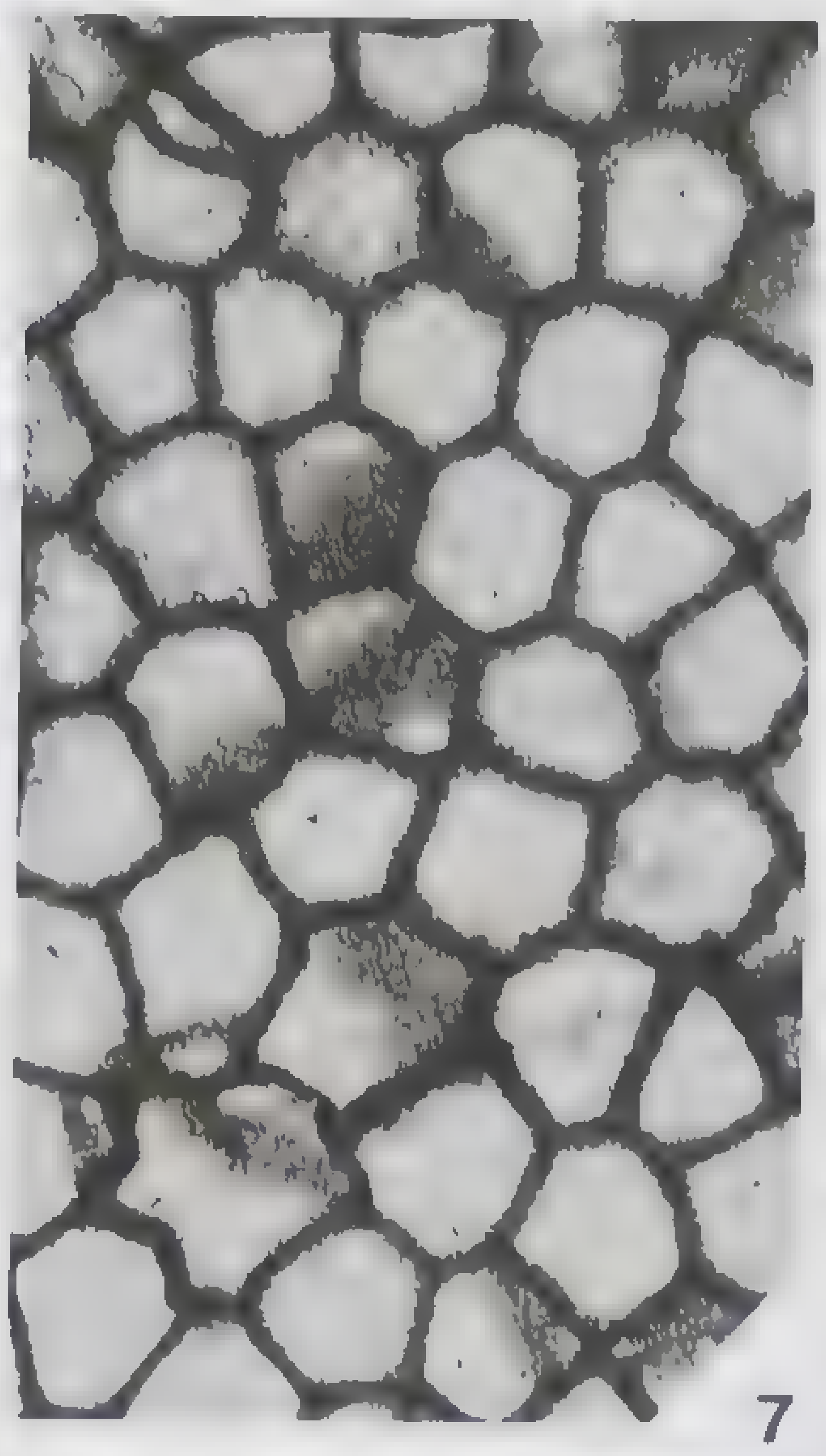
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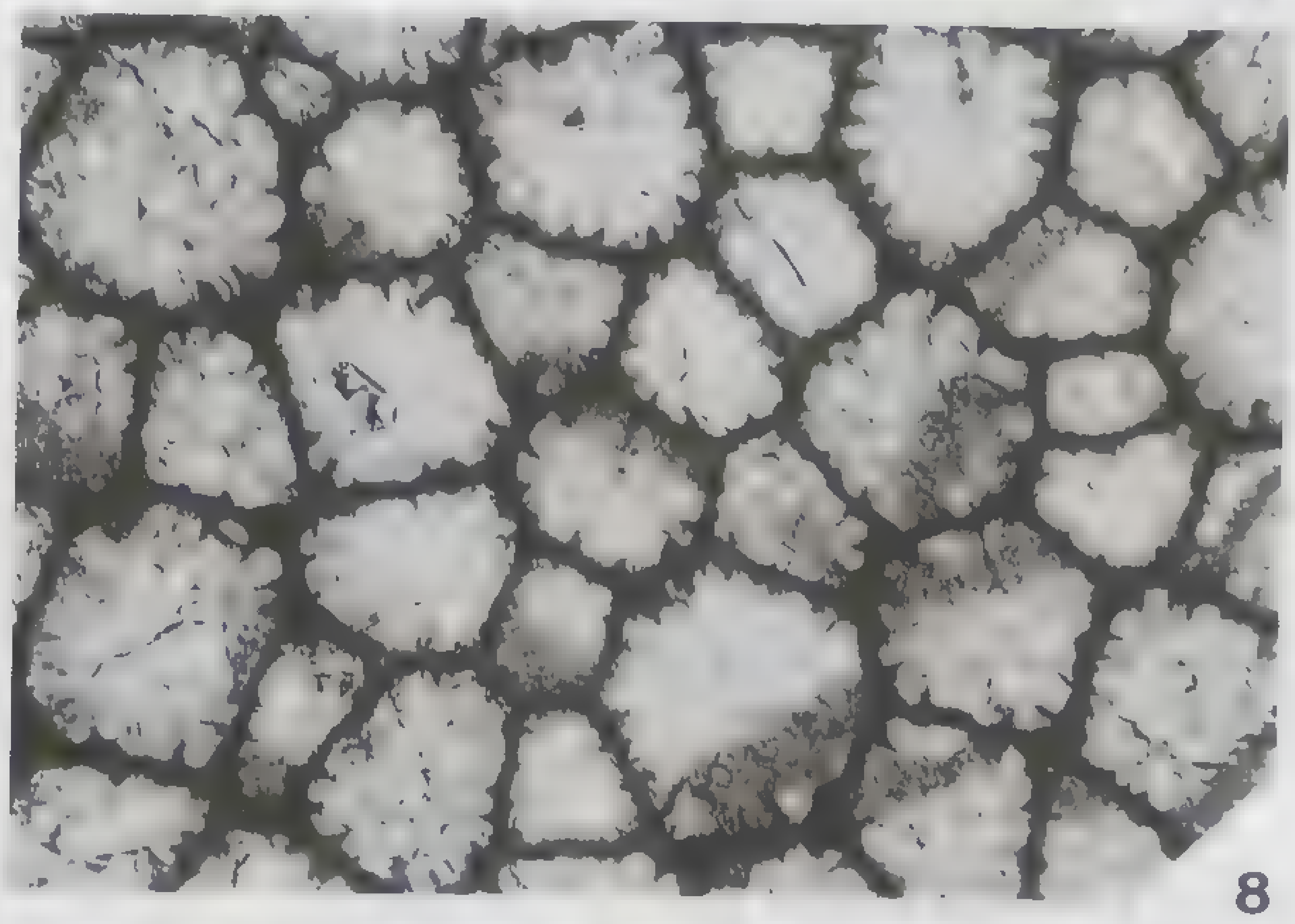
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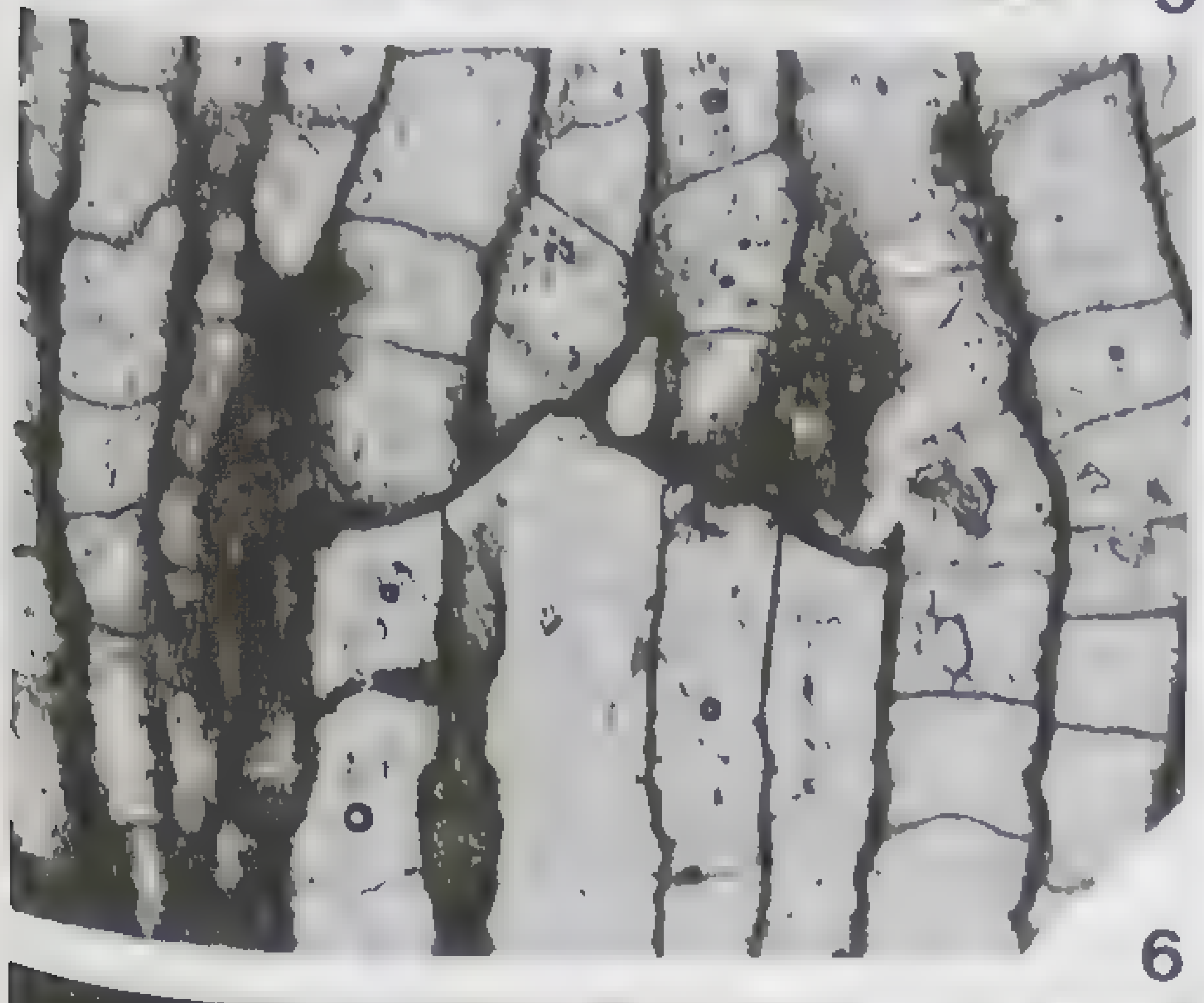
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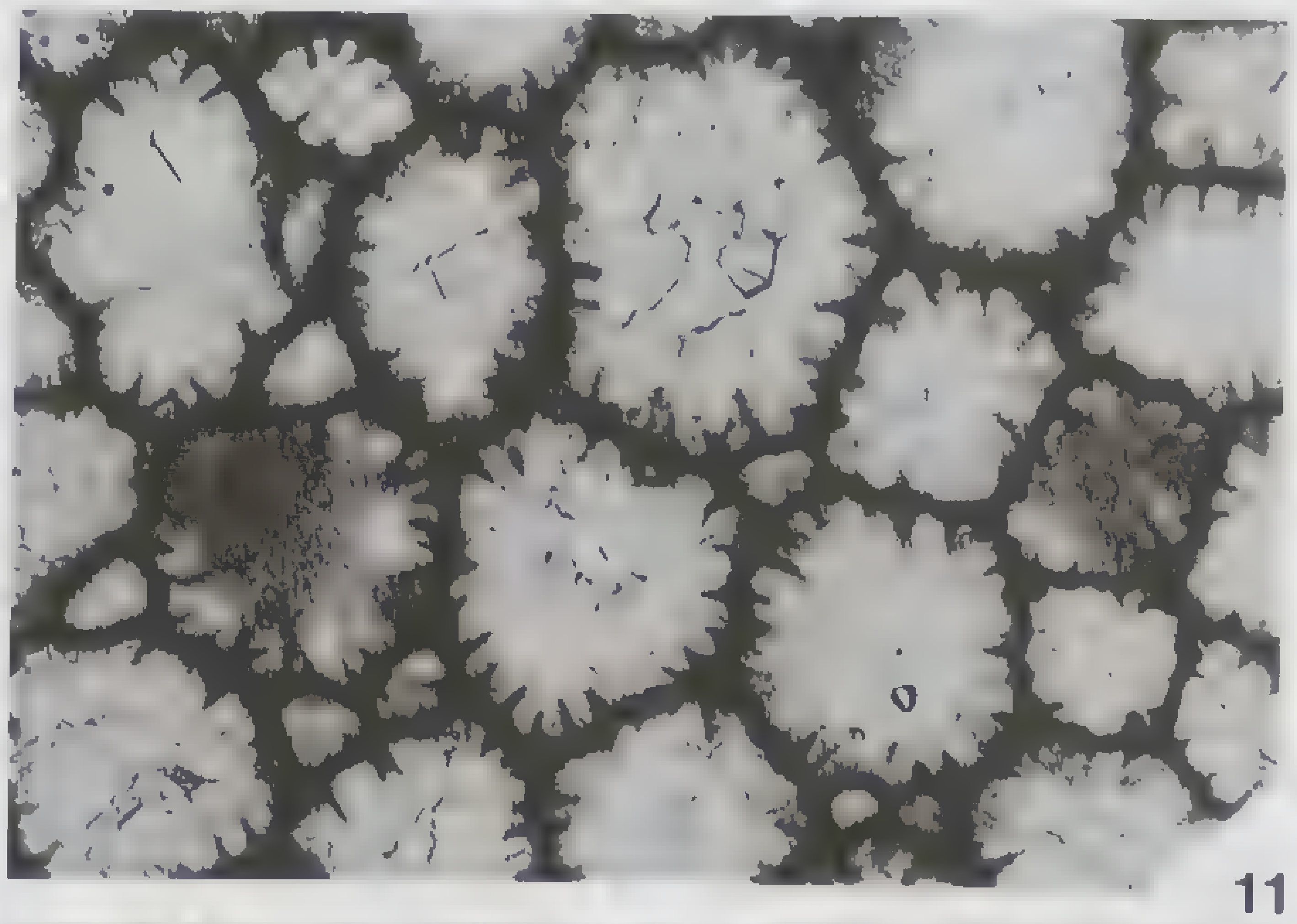
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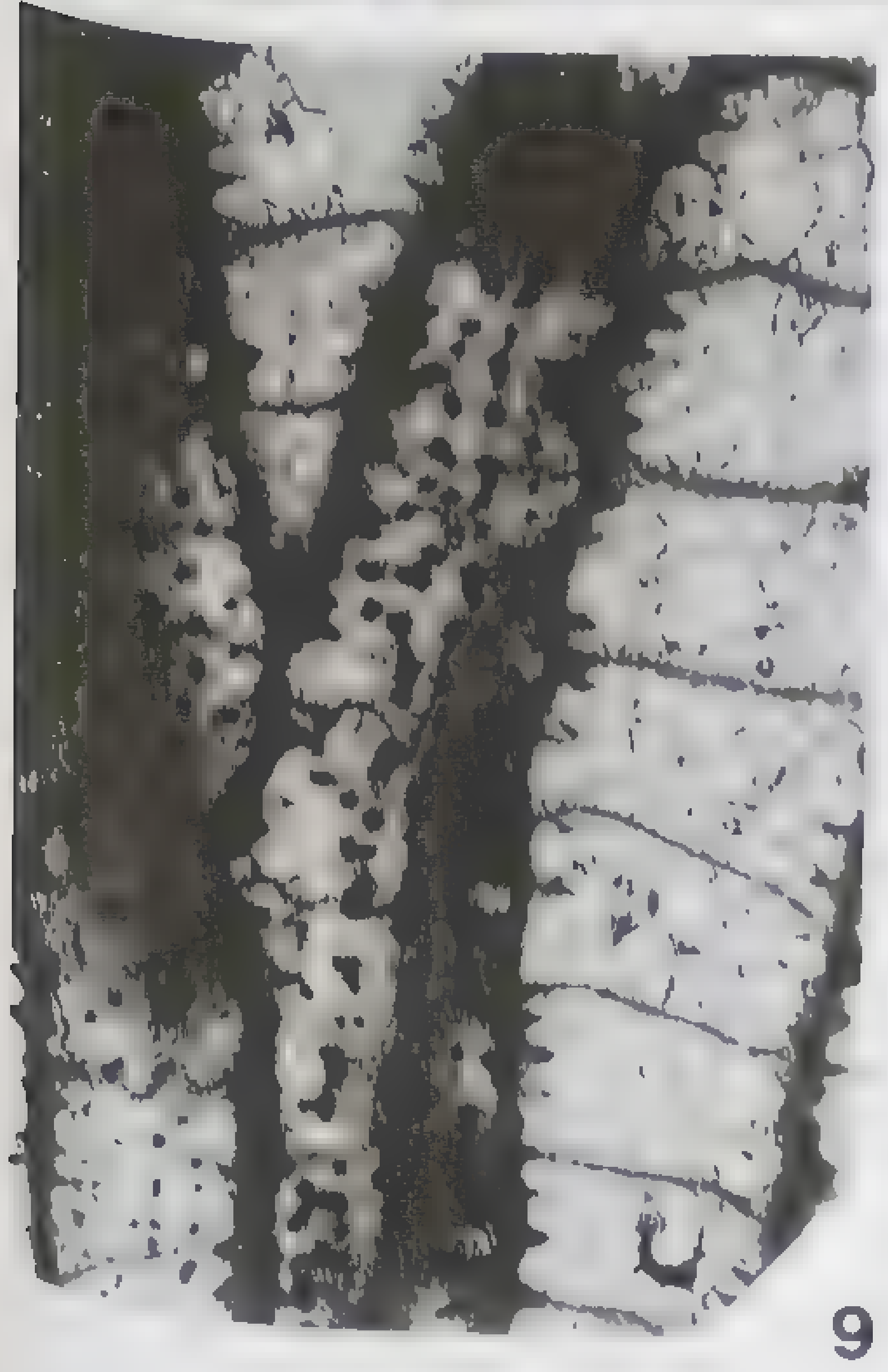
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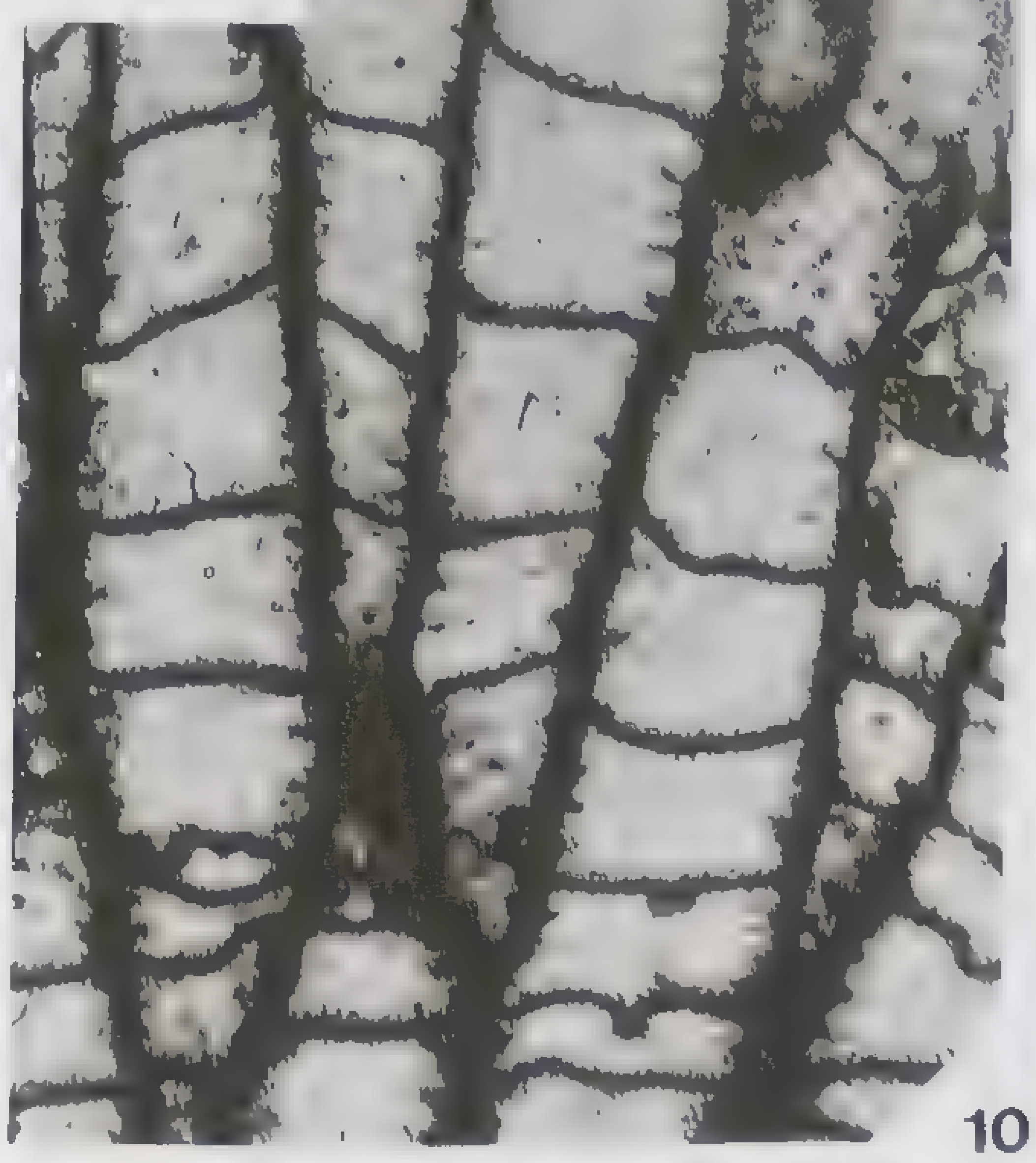
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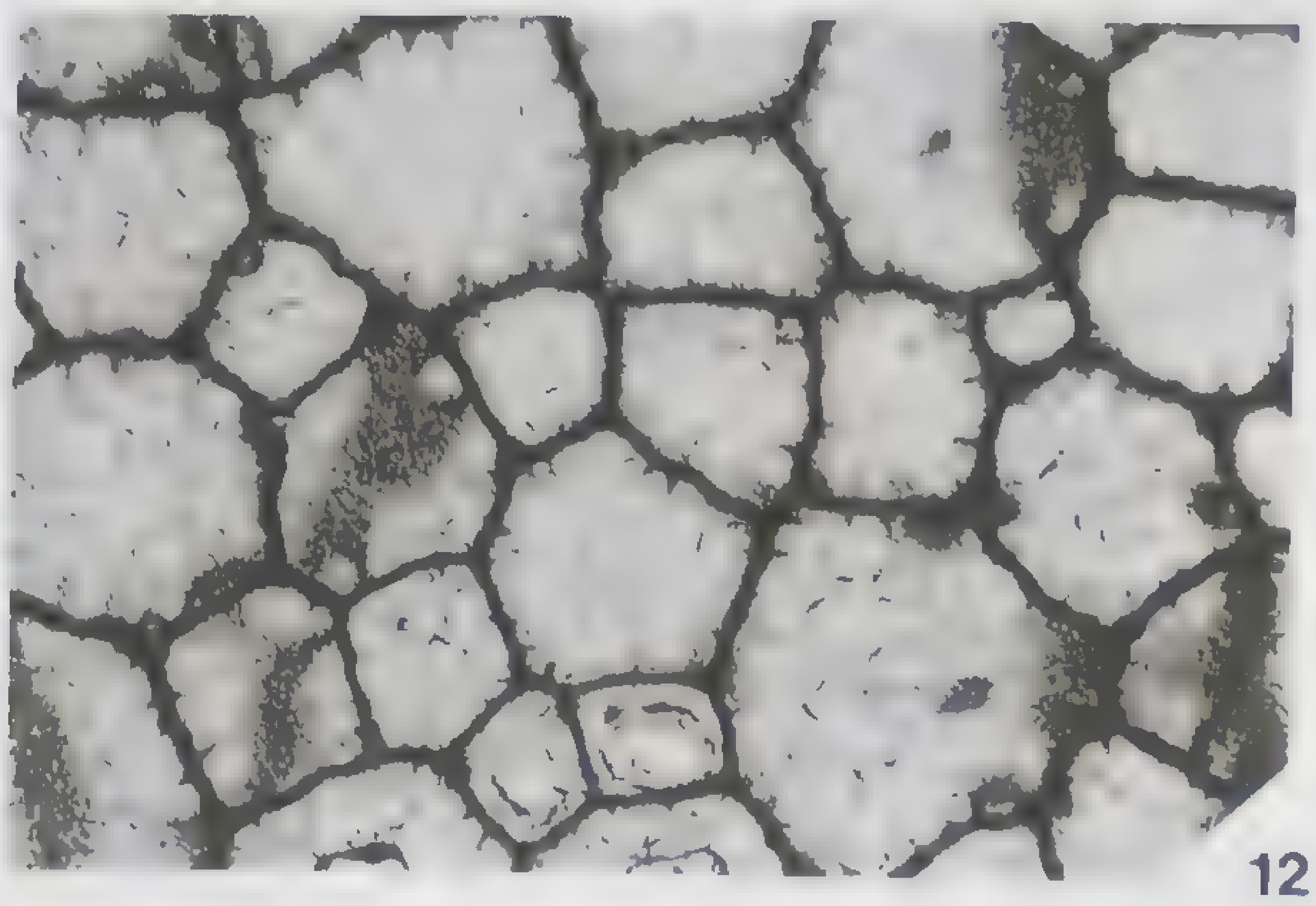
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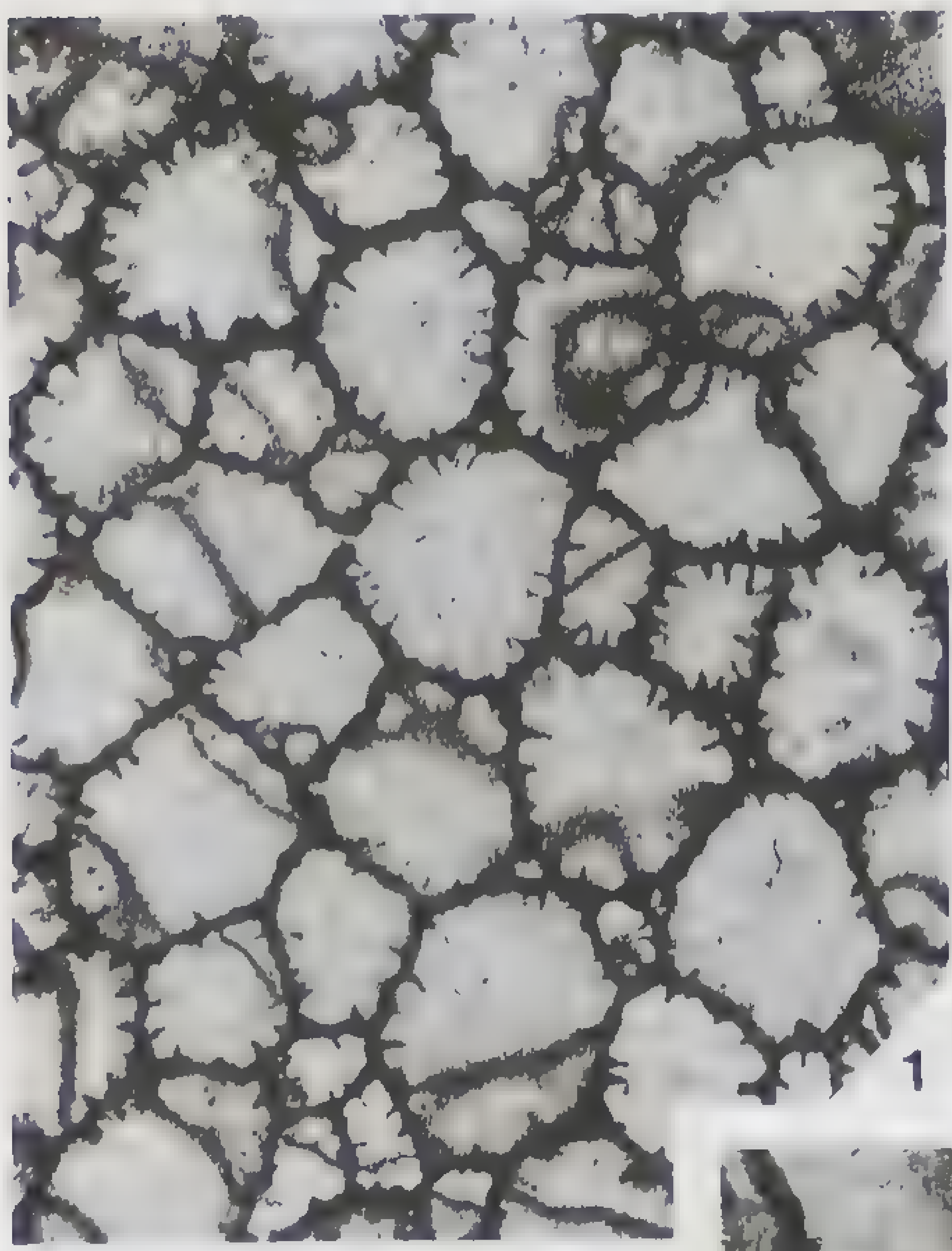
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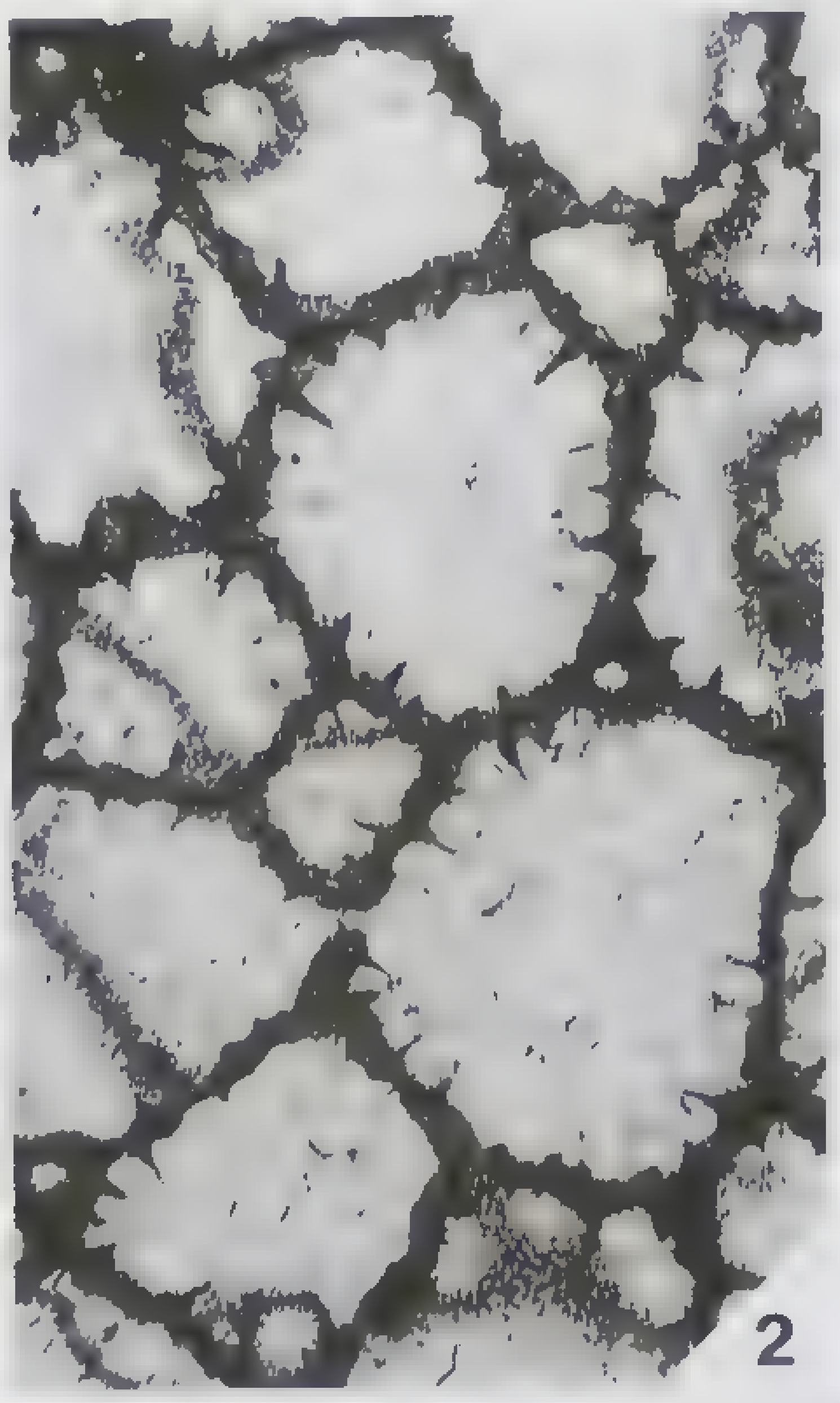
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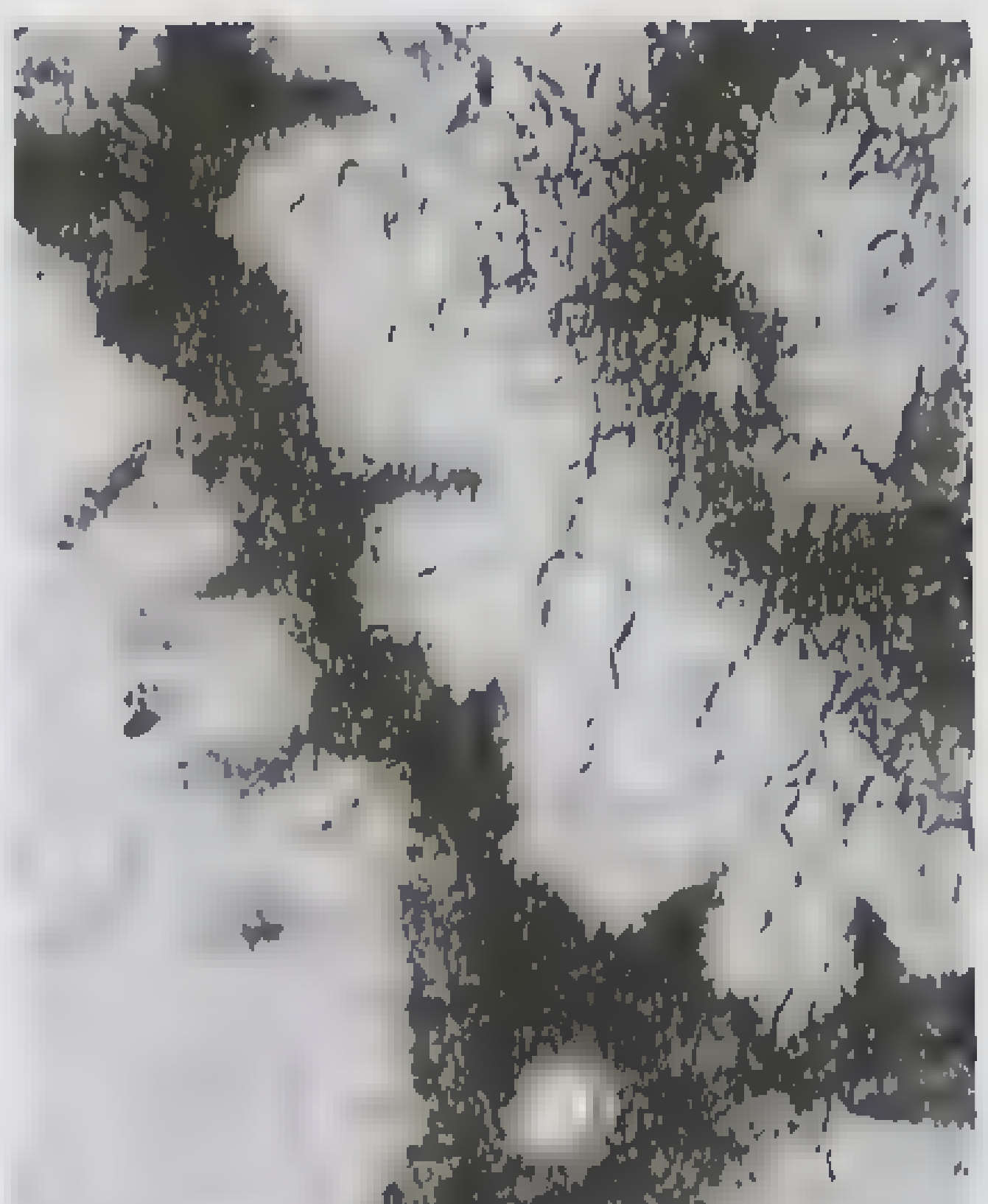
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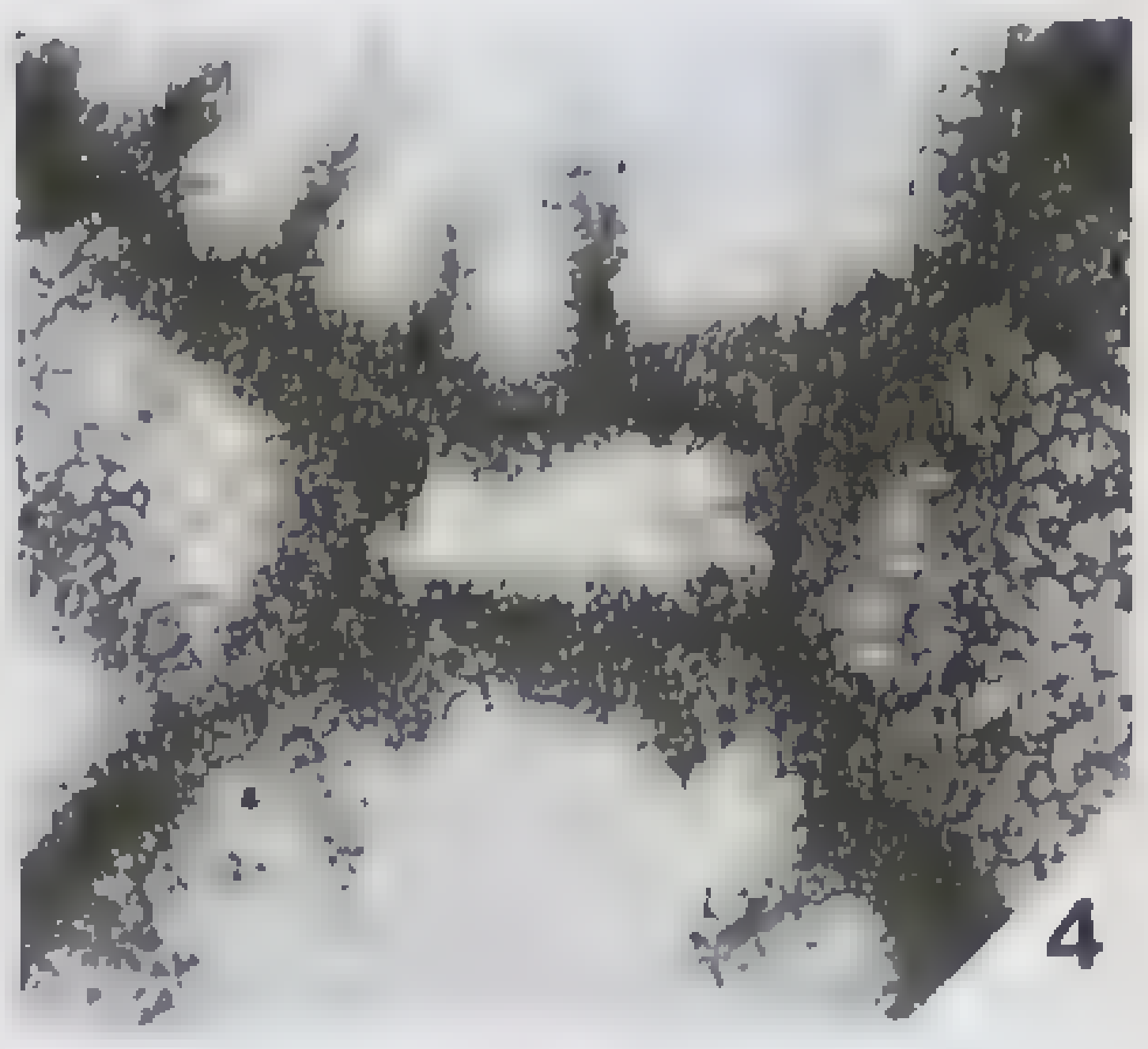
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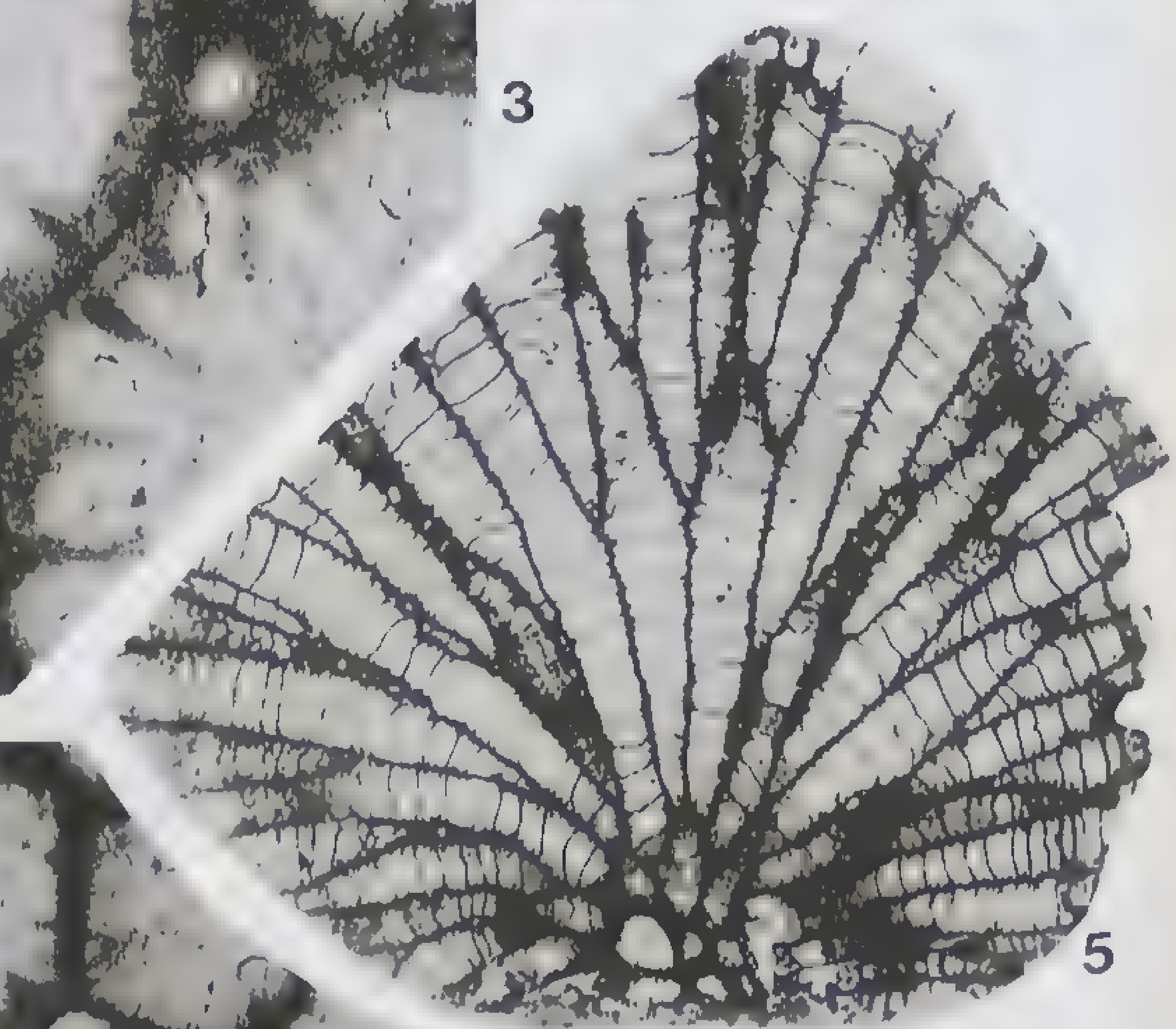
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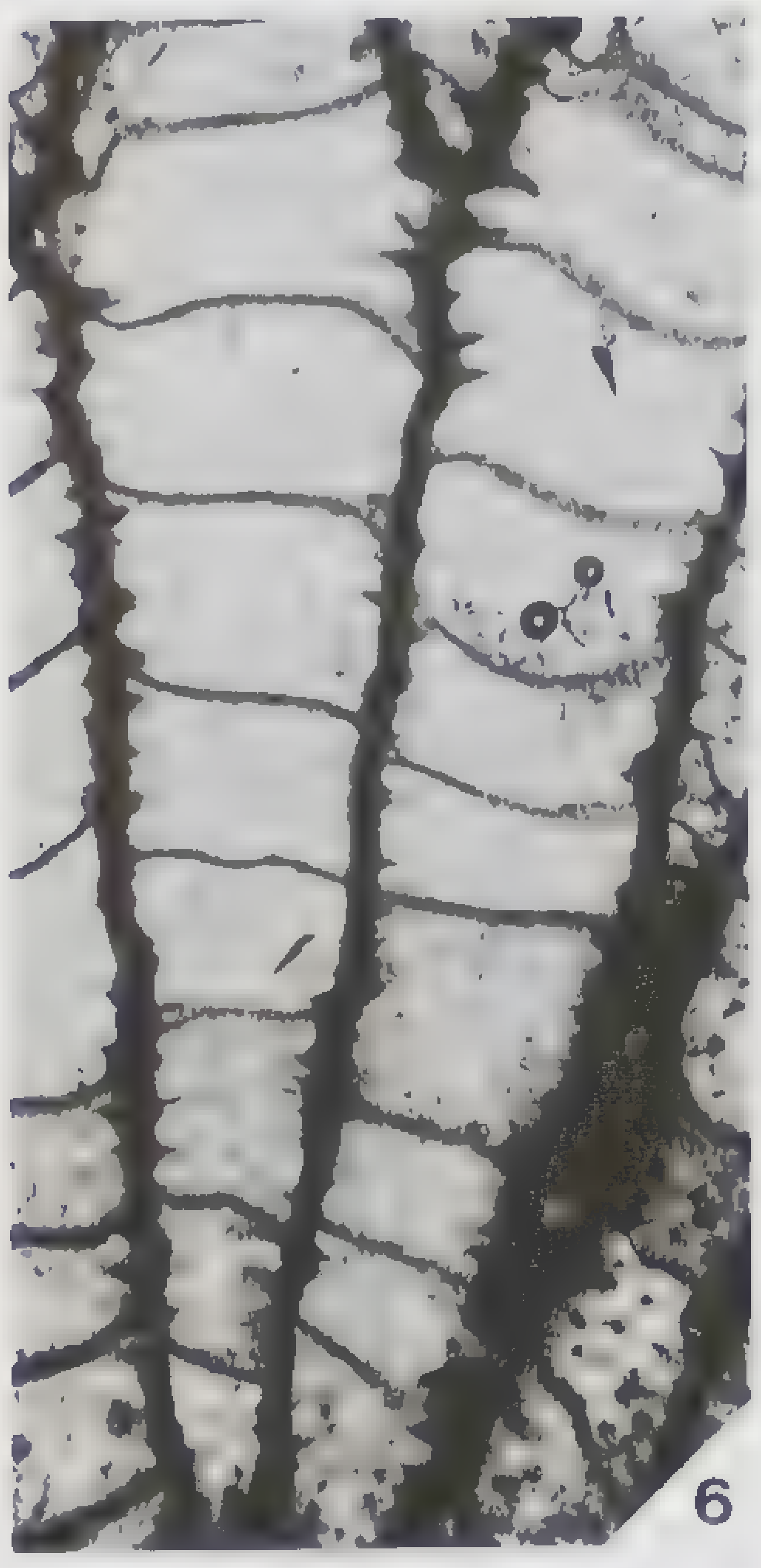
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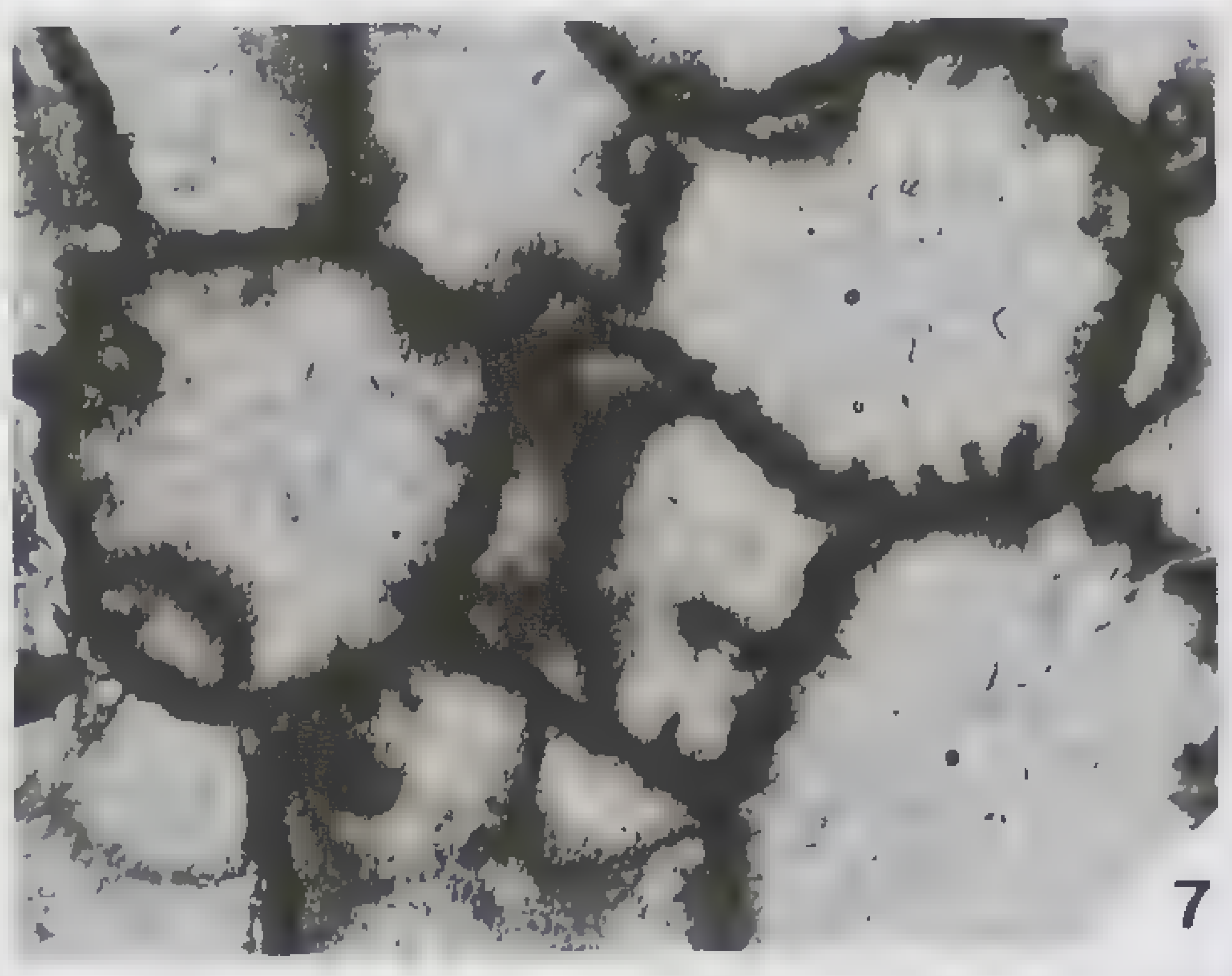
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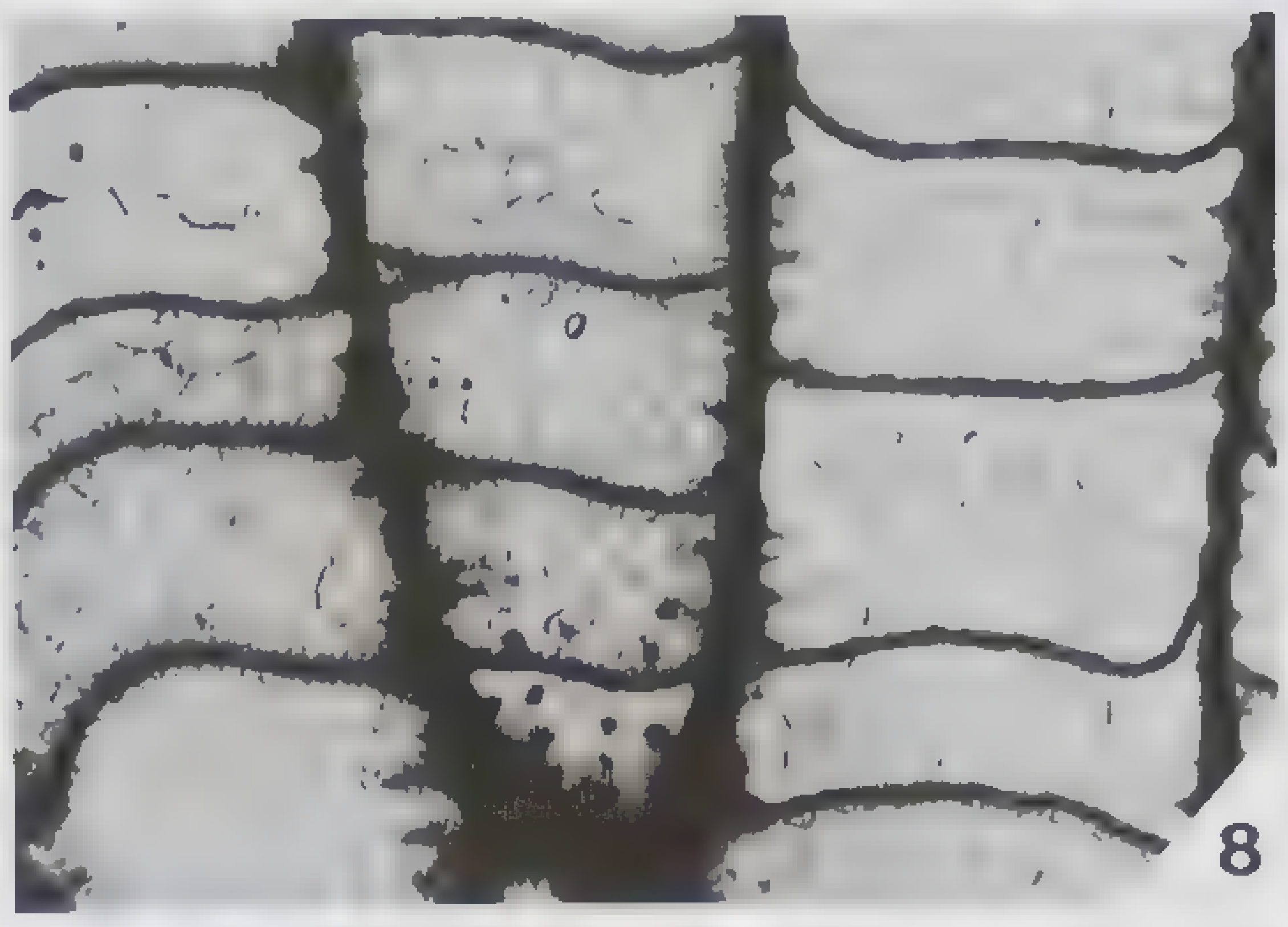
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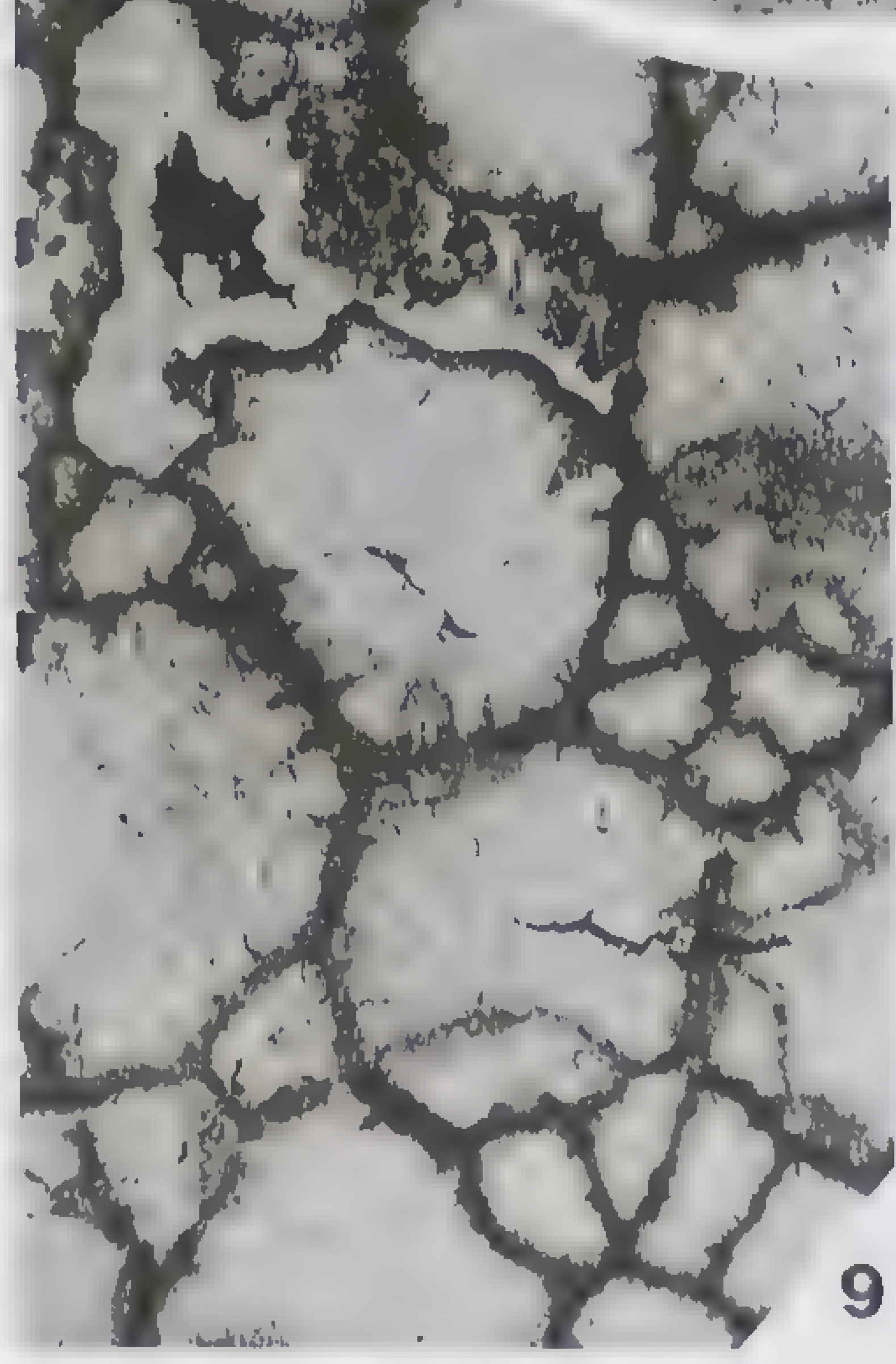
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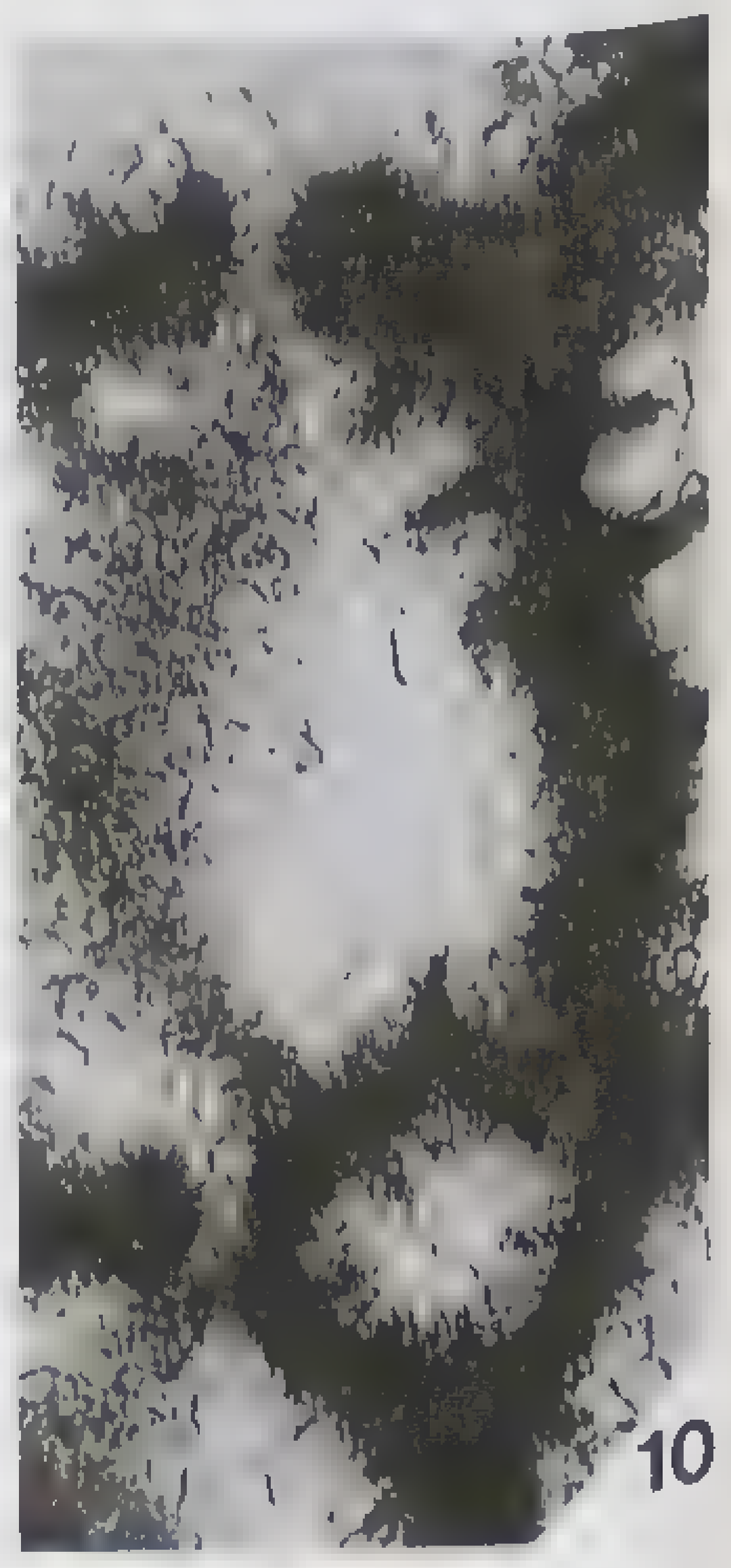
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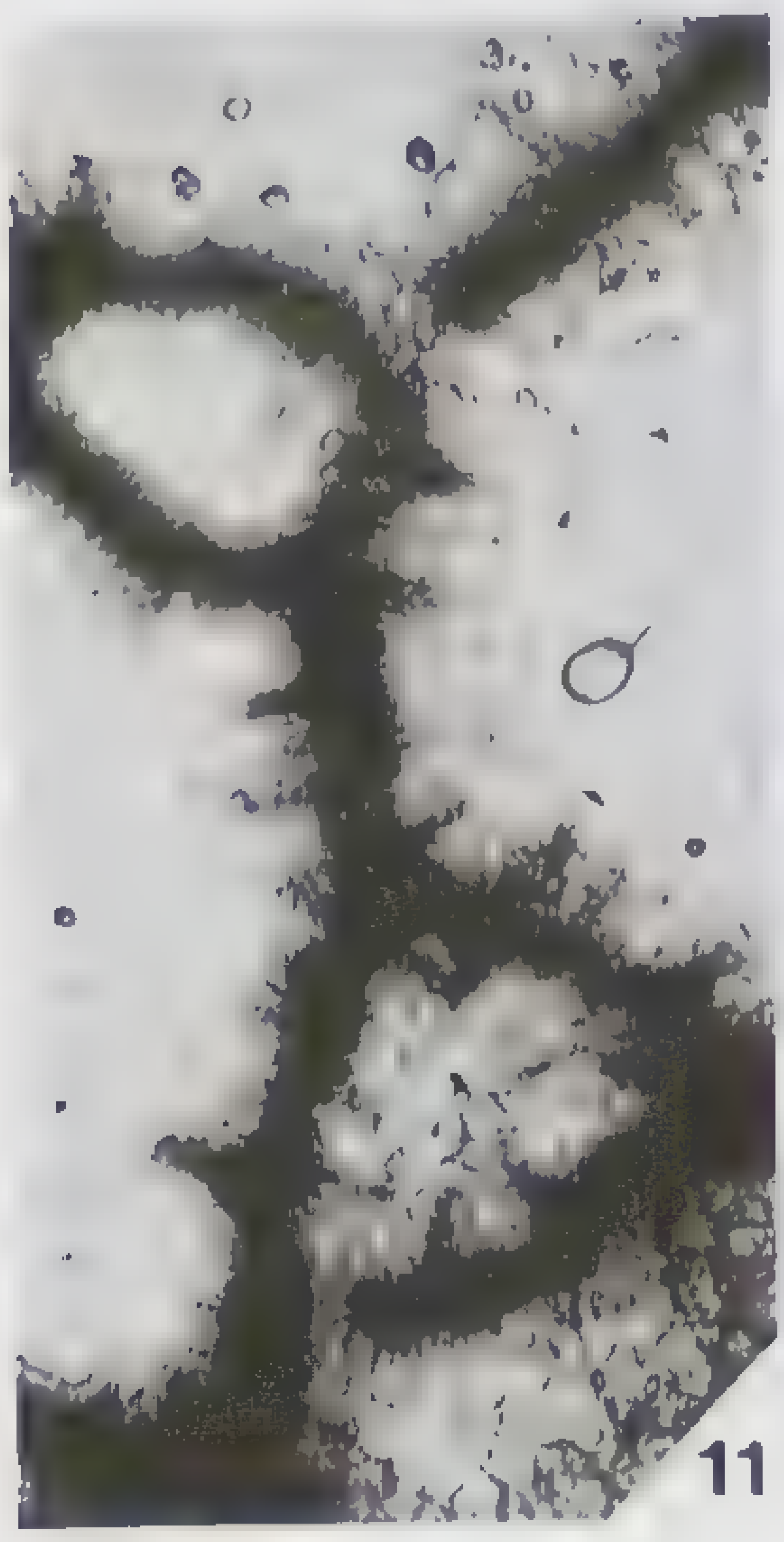
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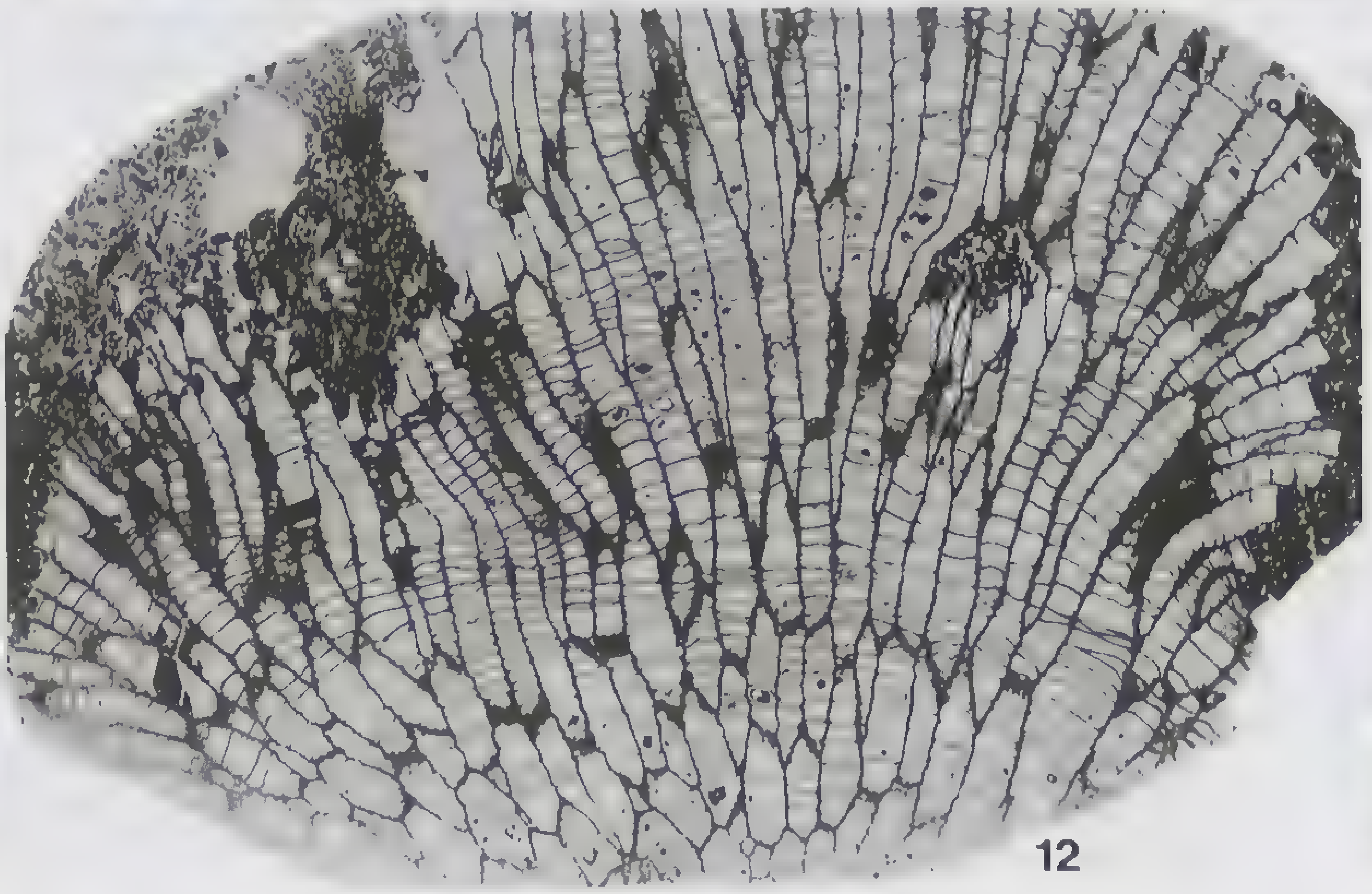
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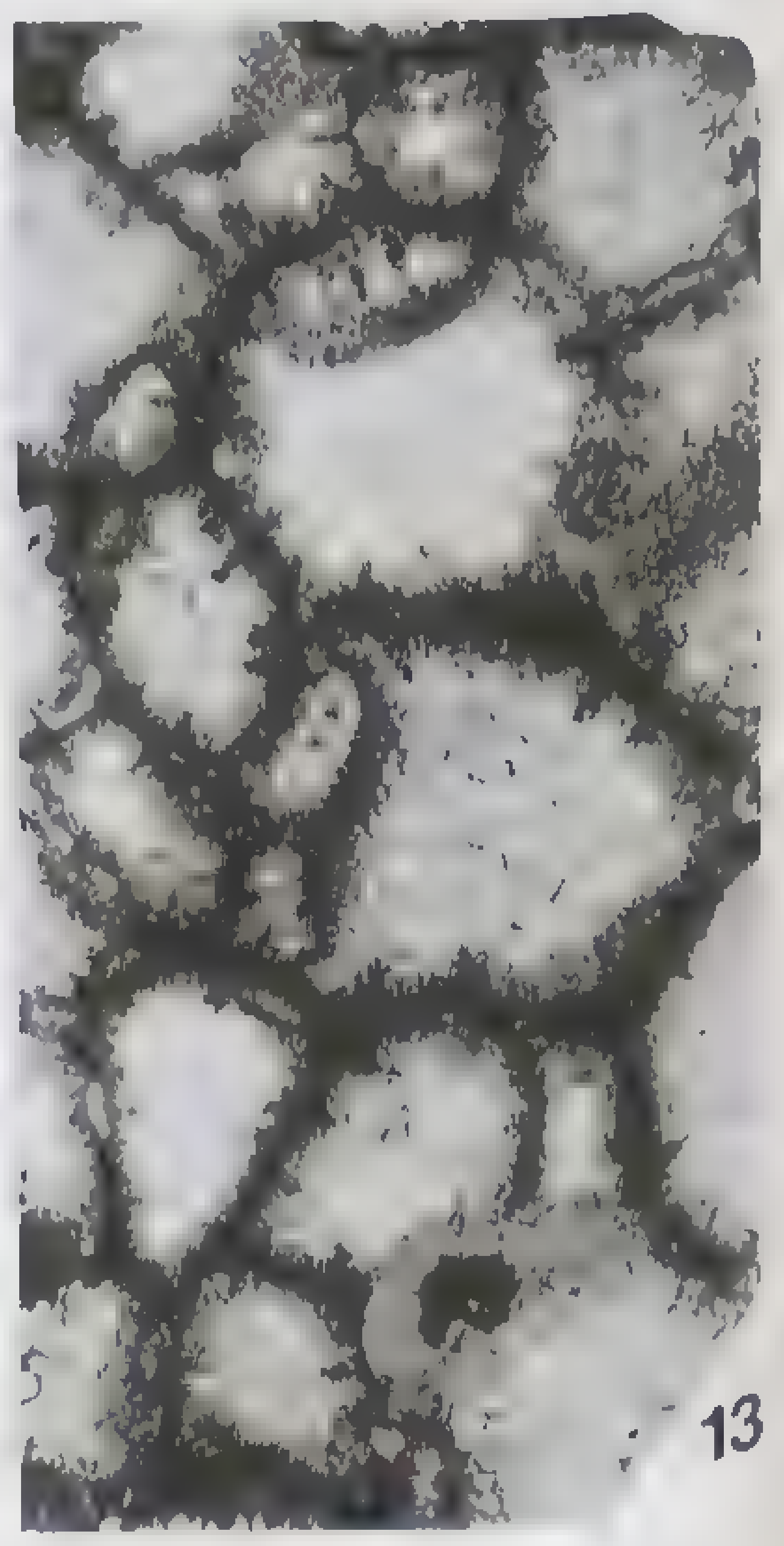
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EXPLANATION OF PLATE 16

Figure | Page

1–13. ***Paleofavosites subelongus*** (Savage, 1913) 78

[1–12, Kissenger Limestone Member, Bryant Knob Formation, Section-interval 14-1 (Higginbotham Farm); 13, Cyrene Formation, Section-interval 13-0 (Bowling Green).]

1–6. USNM 459079: 1, transverse section, ×5; 2, transverse section (detail from upper left of center in 1), ×8; 3, transverse section showing three-sided offset (detail from right of center in 2, turned 30° counterclockwise), ×20; 4, transverse section showing four-sided offset, ×20; 5, longitudinal section through entire corallum, ×2; 6, longitudinal section (detail from center in 5, turned 10° clockwise), ×8.

7, 8. USNM 485866: 7, transverse section, ×8; 8, longitudinal section, ×8.

9. USNM 485839: transverse section showing regeneration following partial mortality, ×8.

10. USNM 485860: transverse section showing corner pore, mid-wall pore, and offset, ×20.

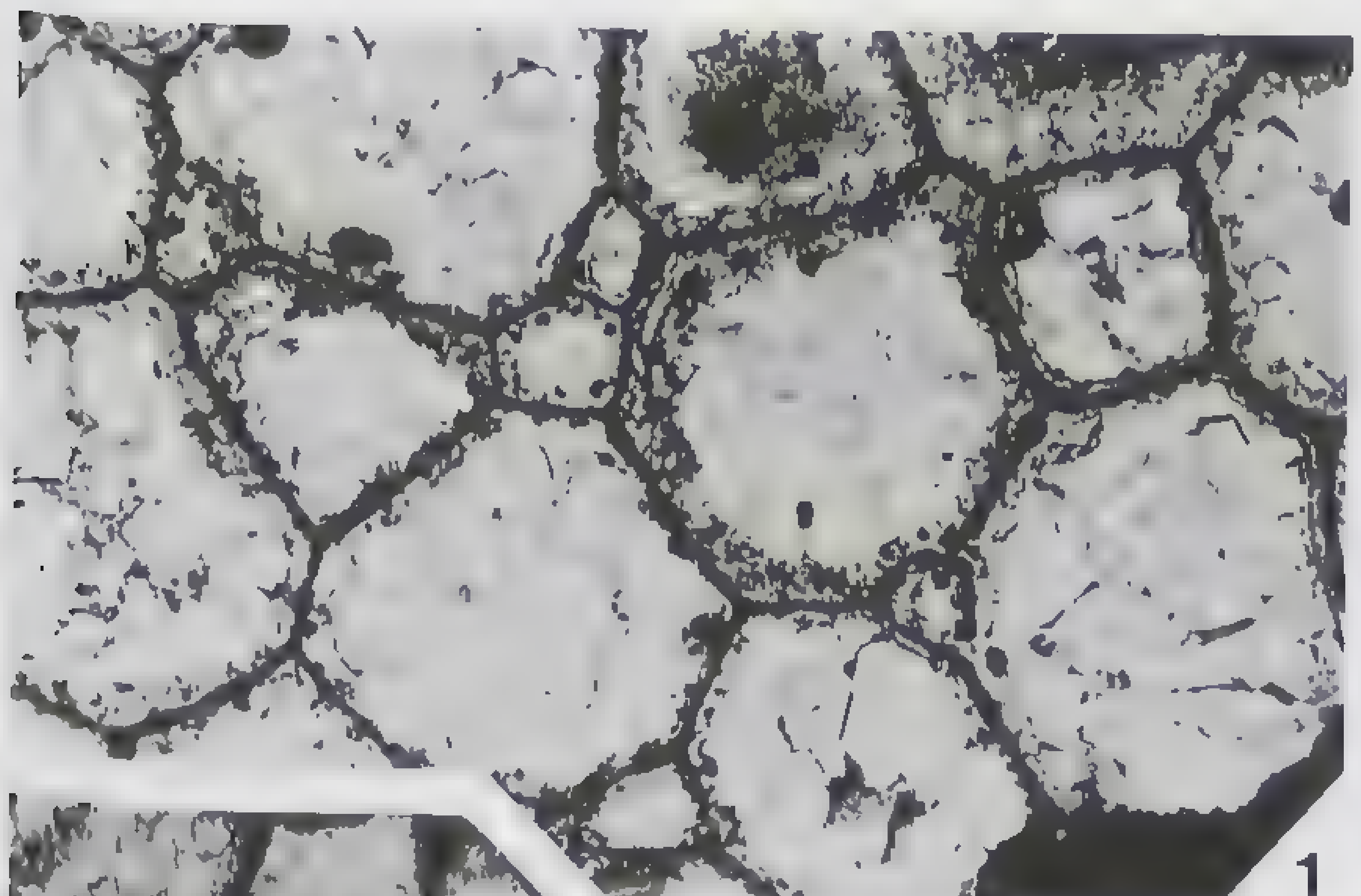
11. USNM 485846: transverse section showing offsets and corner pores, ×20.

12. USNM 485858c: longitudinal section through entire corallum (note abraded upper surface on left side), showing cyclomorphic variation in spacing of tabulae, ×1.5.

13. USNM 485874: transverse section, ×8.

EXPLANATION OF PLATE 17

Figure		Page
1–7.	***Paleofavosites subelongus*** (Savage, 1913)	78
	[1–3, Wilhelmi Formation, Section-interval 37-1 (Essex); 4–7, coral-rich bedding surface of Mosalem Formation, Section-interval 32-1z (Thomson East).]	
	1–3. USNM 485877: 1, transverse section, ×8; 2, transverse section showing three-way corner pore, ×20; 3, longitudinal section, ×8.	
	4, 5. USNM 485886: 4, transverse section, ×8; 5, longitudinal section, ×8.	
	6, 7. USNM 485897: 6, transverse section ×8; 7, longitudinal section, ×8.	
8–12.	***Paleofavosites*** species cf. ***P. subelongus*** (Savage, 1913)	89
	[8–12, upper Mosalem Formation, Section-interval 32-1c (Thomson East).]	
	8. USNM 485930: transverse section showing mid-wall pore, ×20.	
	9, 10. USNM 485929: 9, transverse section, ×8; 10, longitudinal section, ×8.	
	11, 12. USNM 485934: 11, transverse section, ×8; 12, longitudinal section, ×8.	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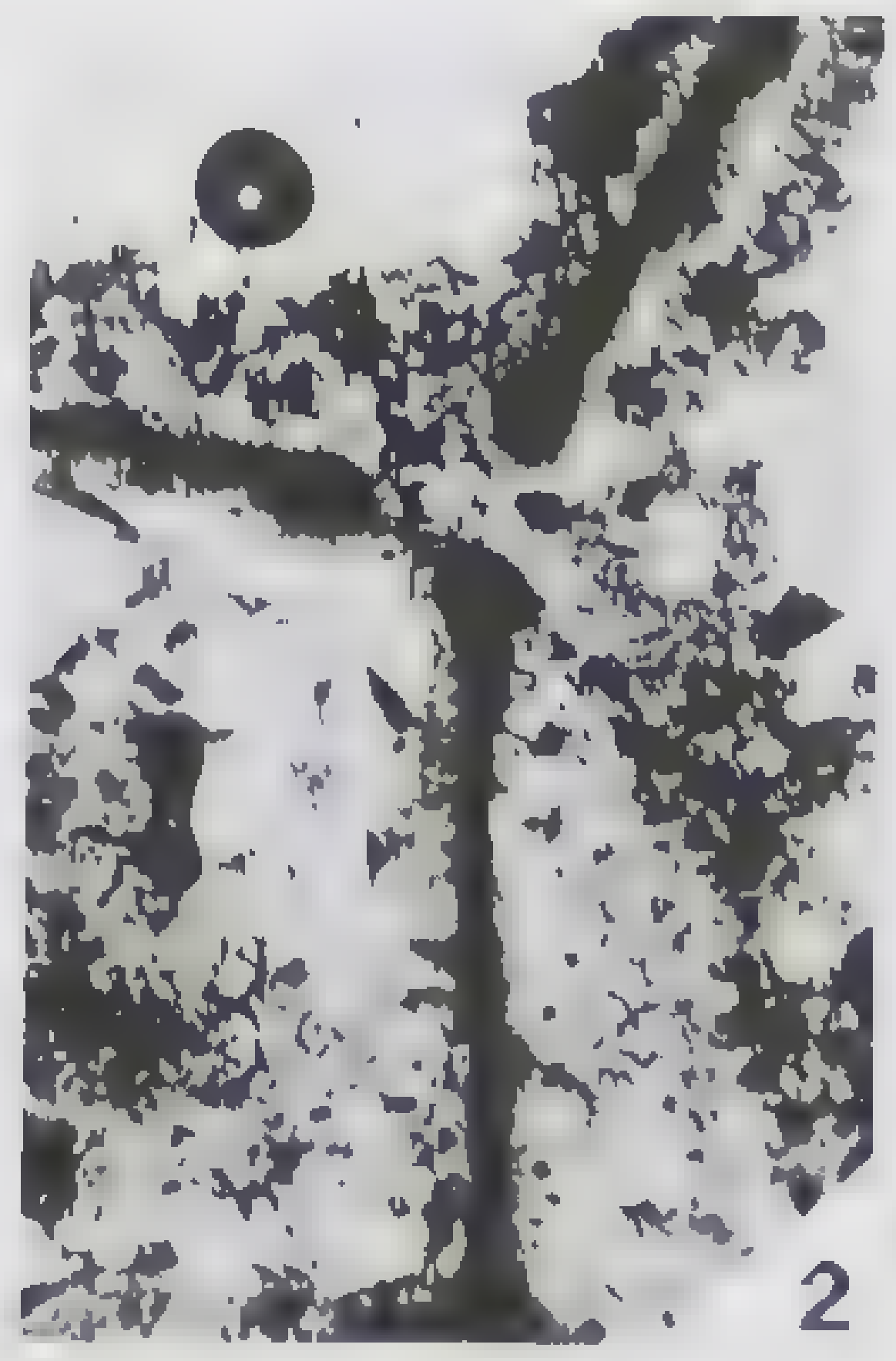
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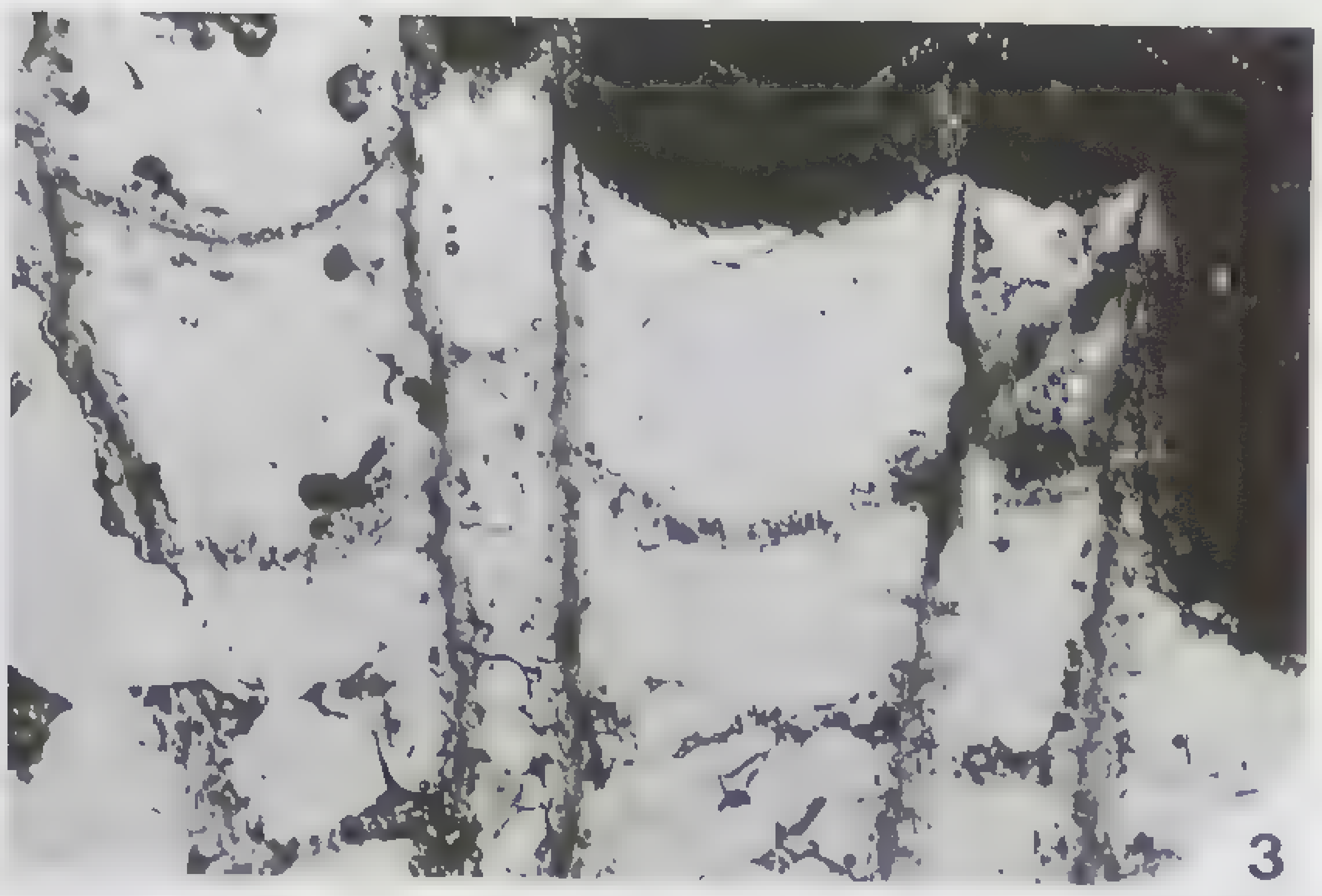
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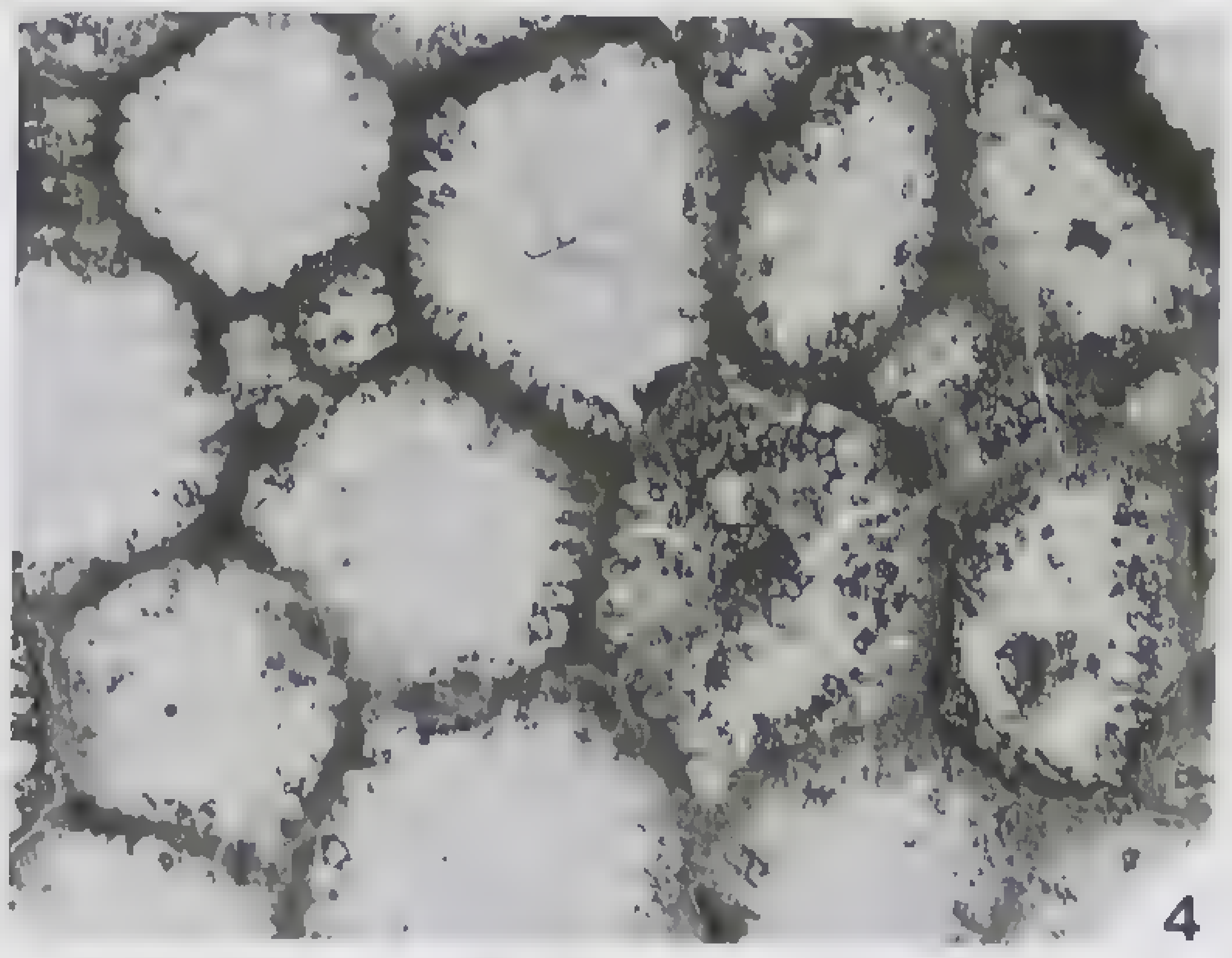
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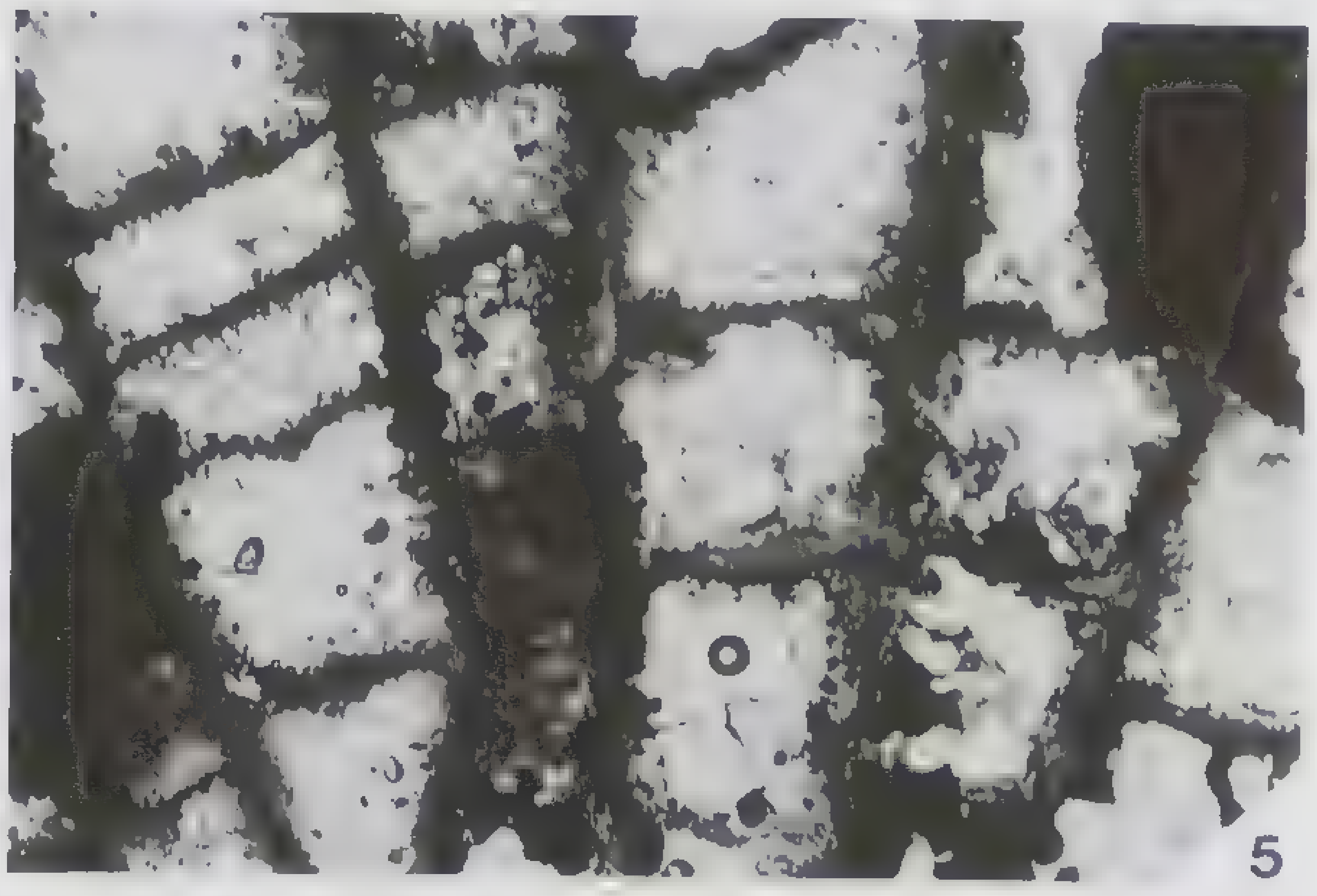
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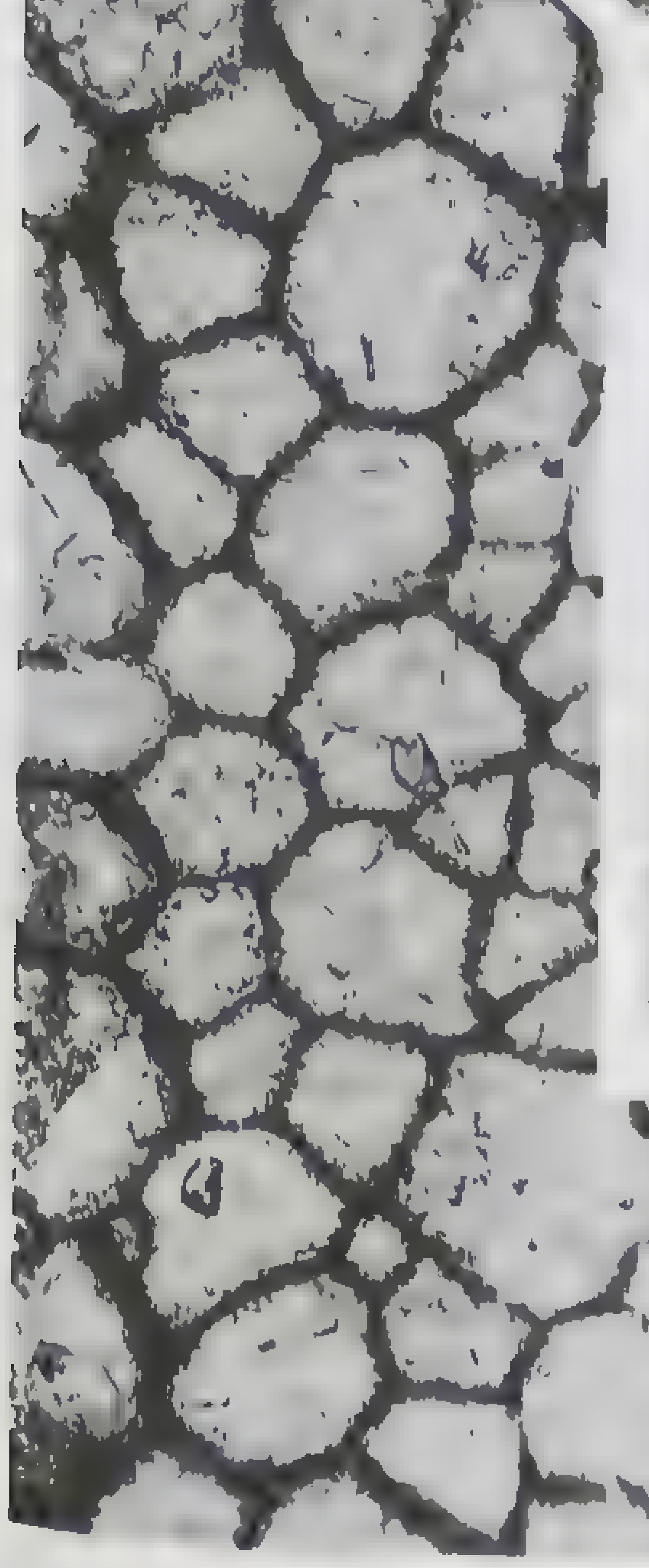
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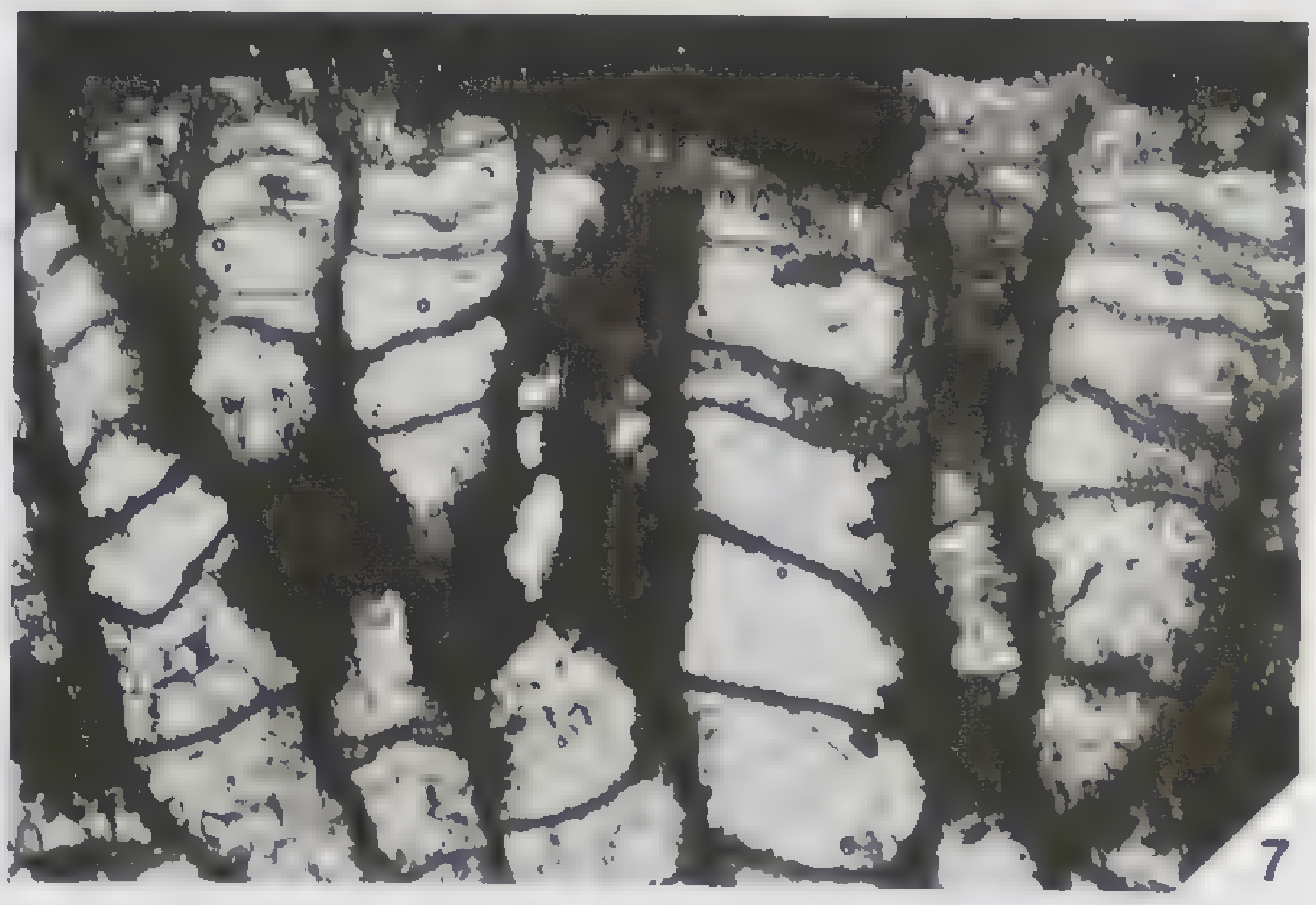
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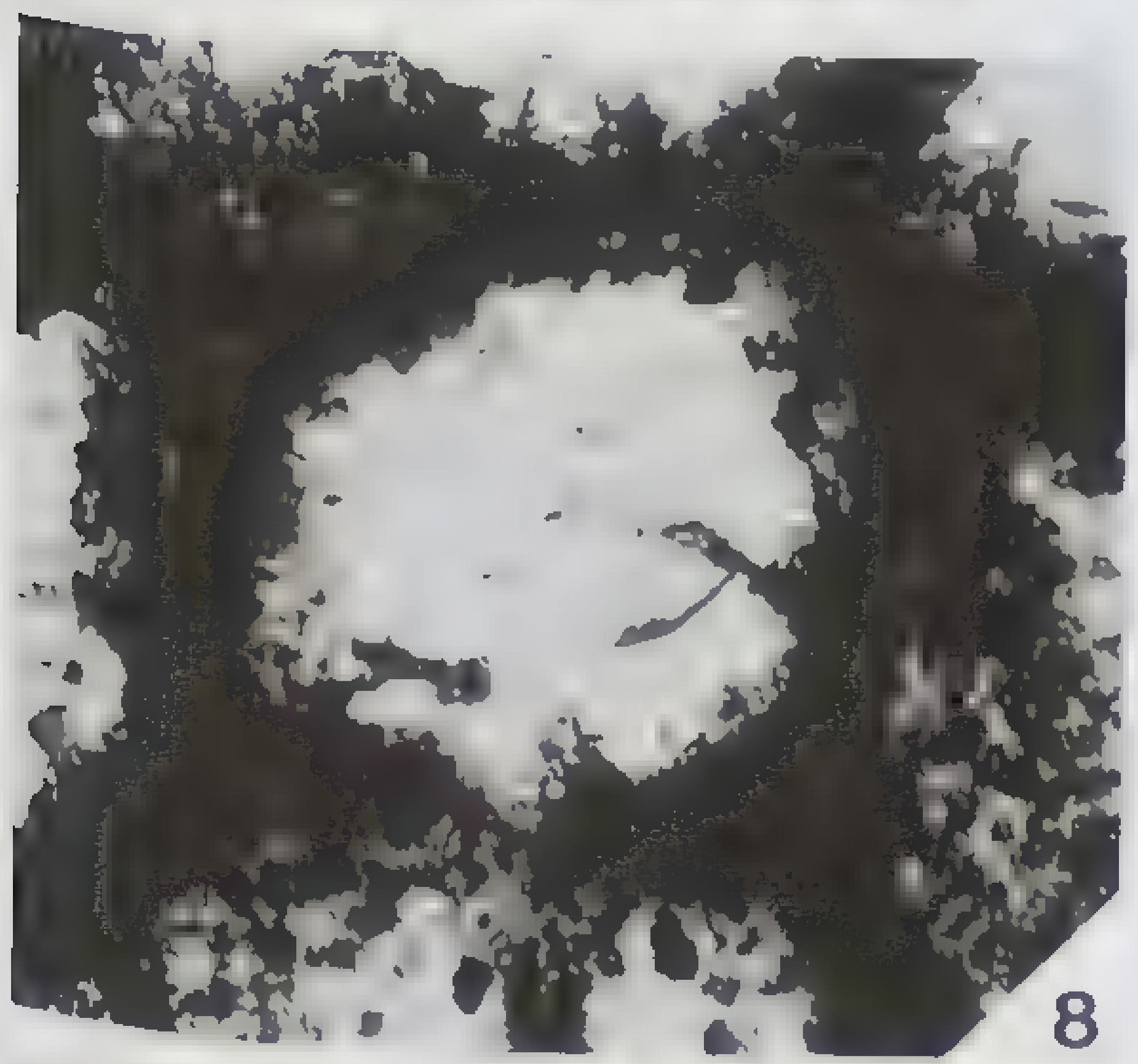
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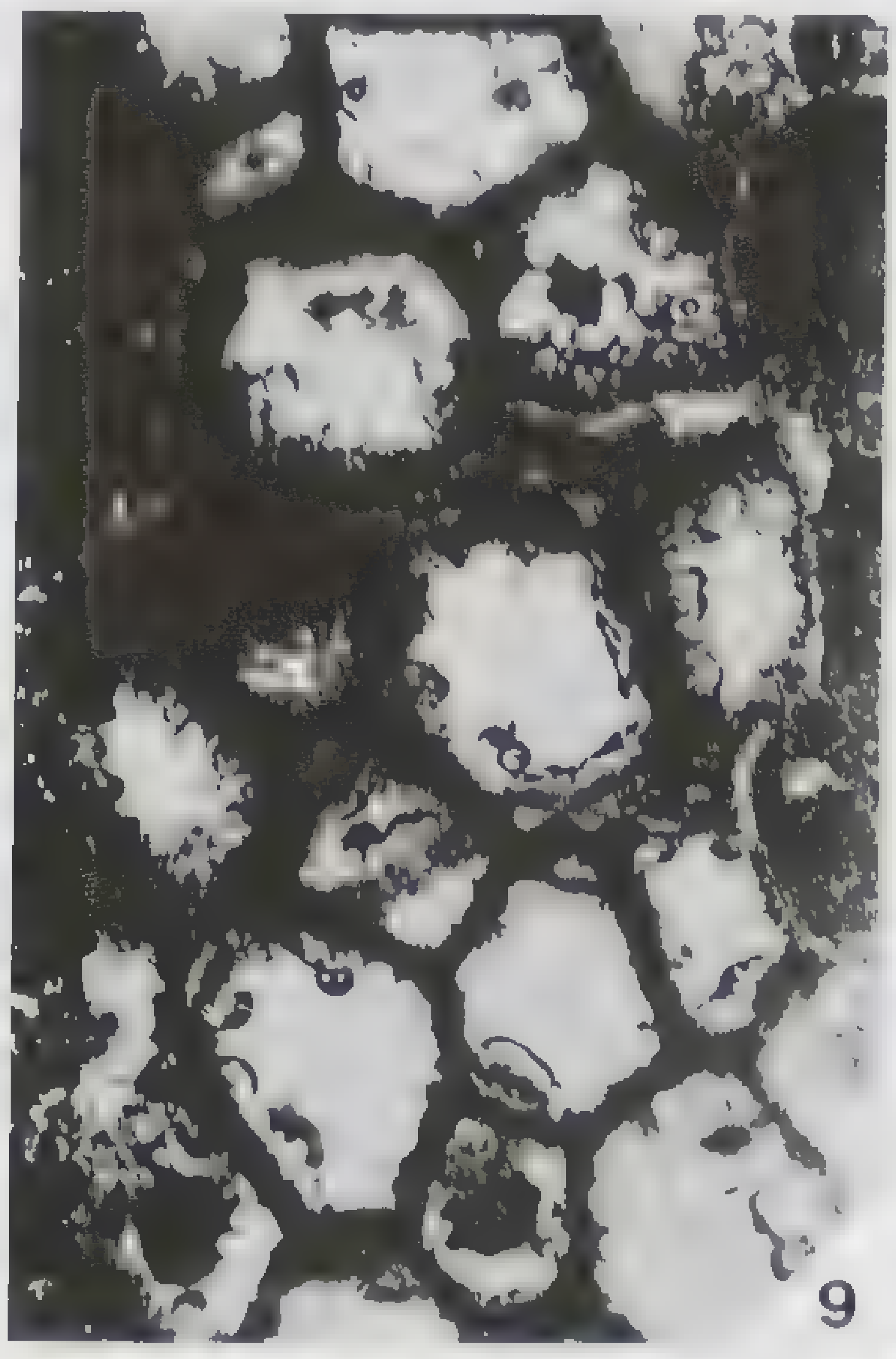
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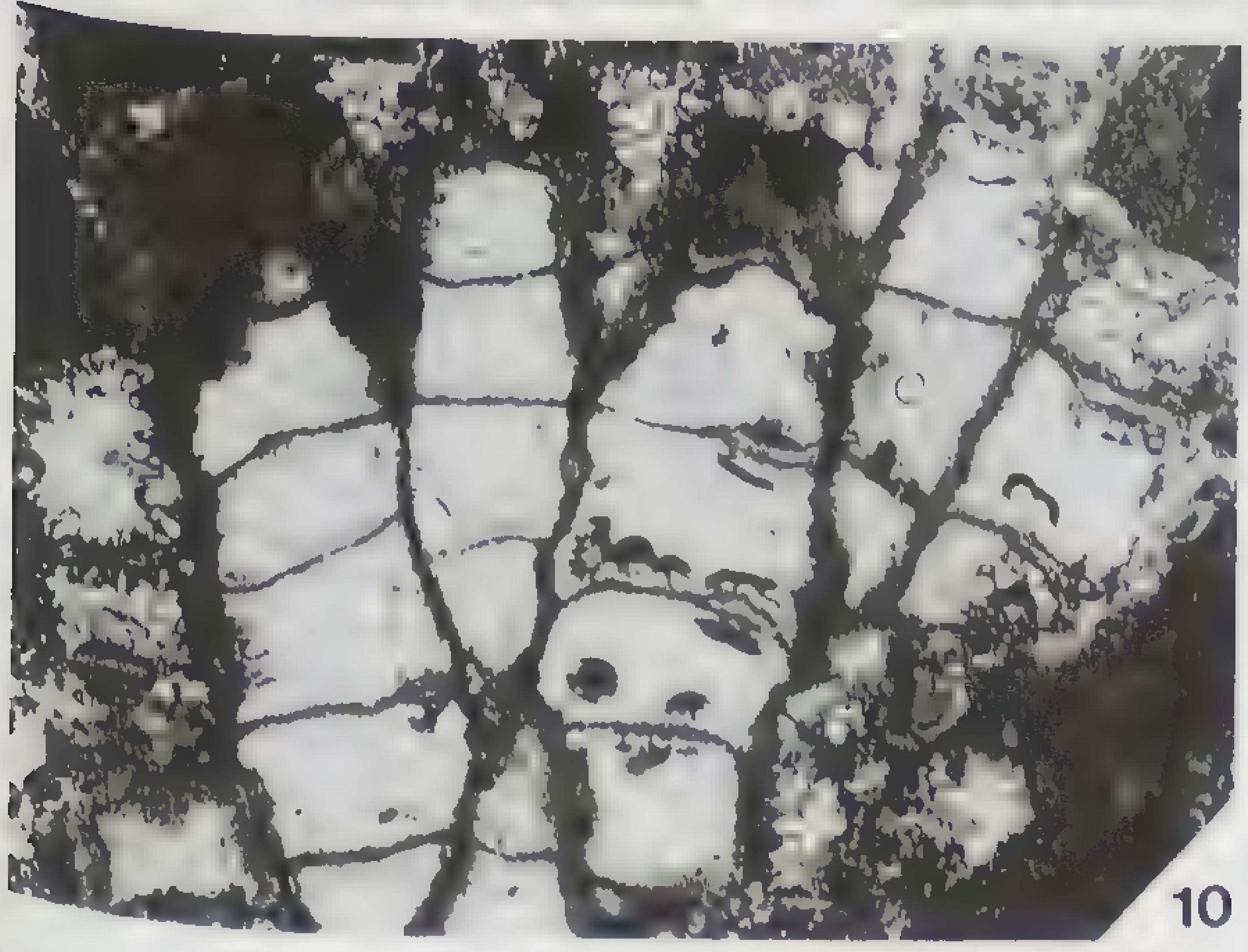
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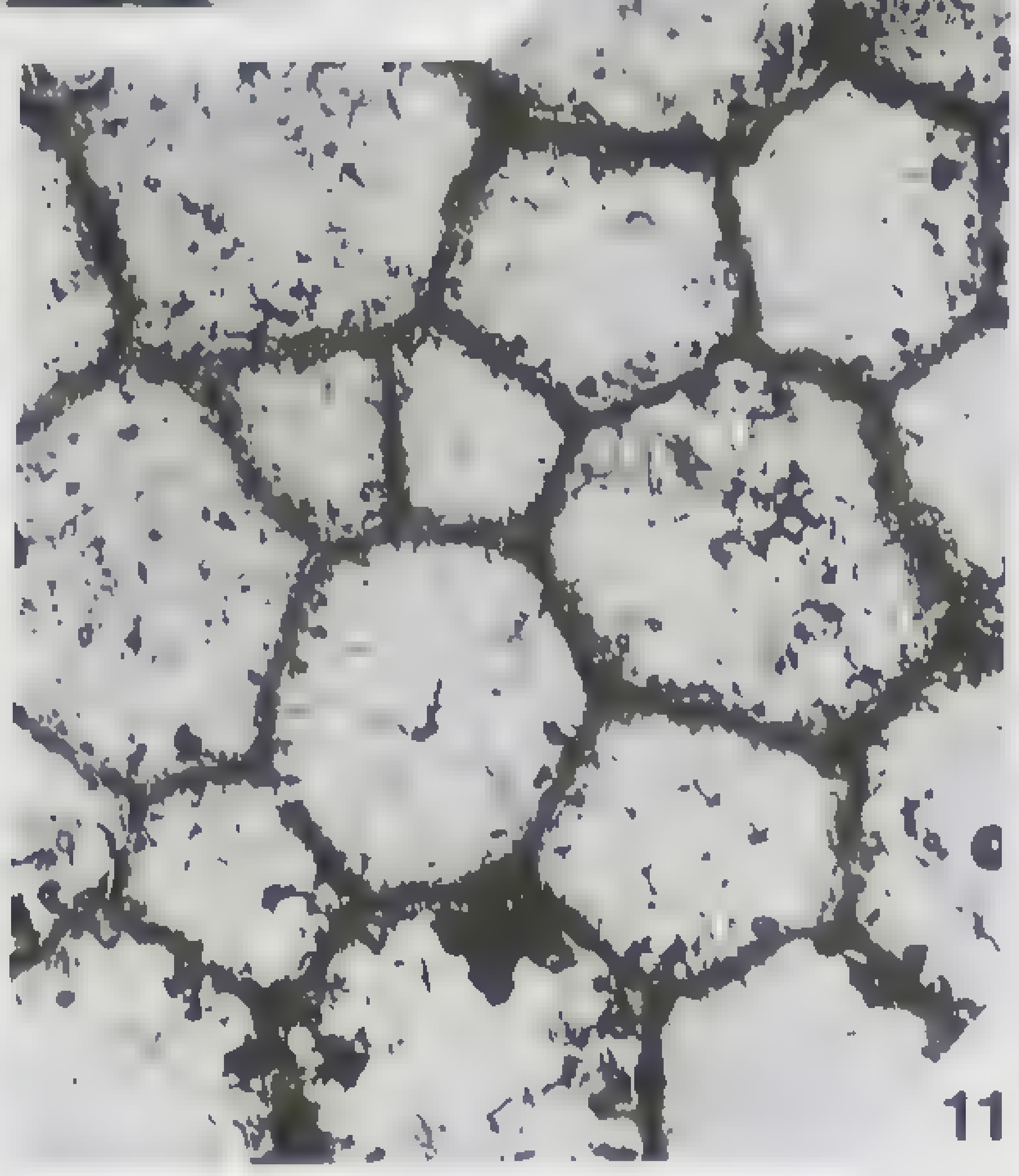
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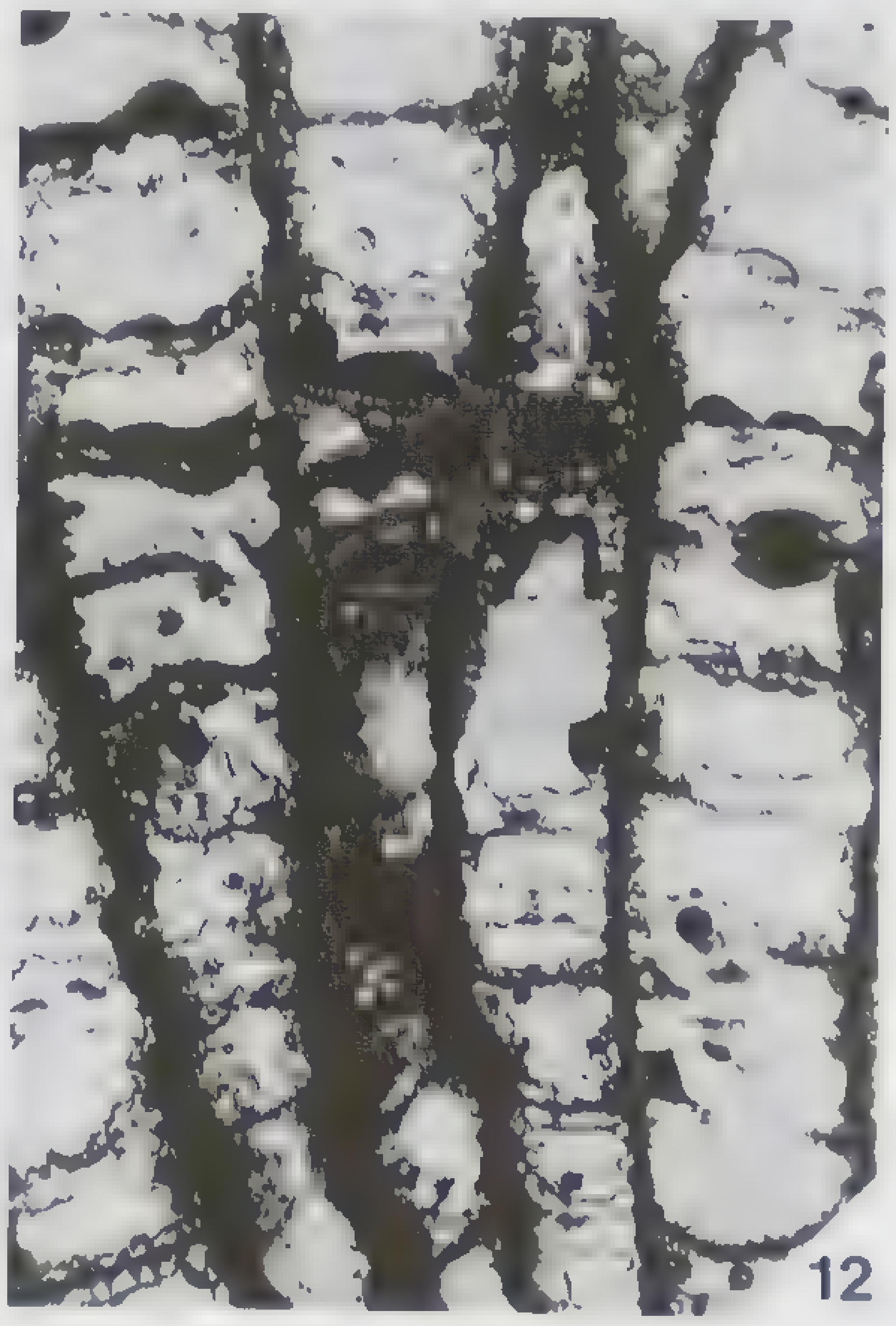
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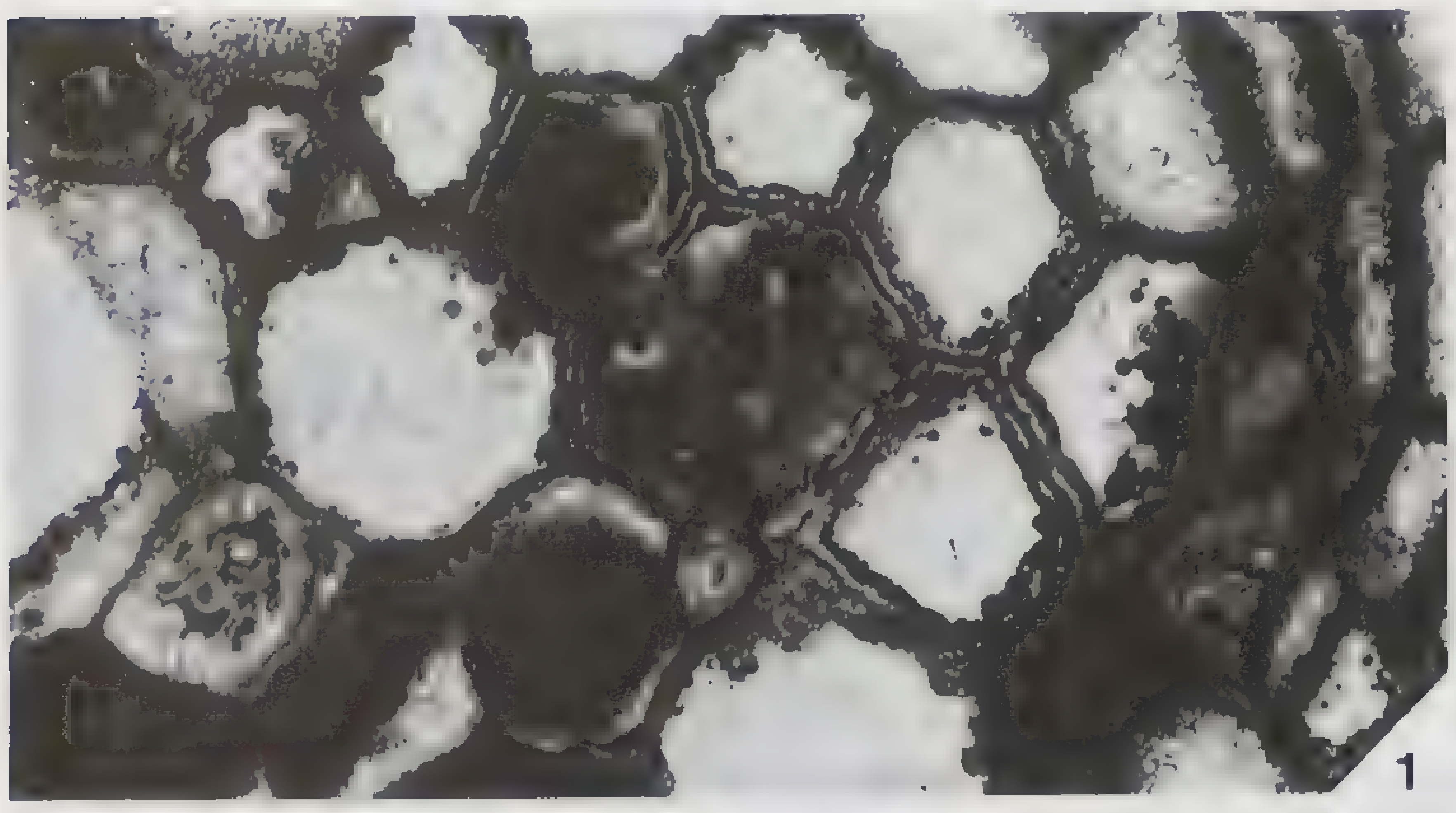
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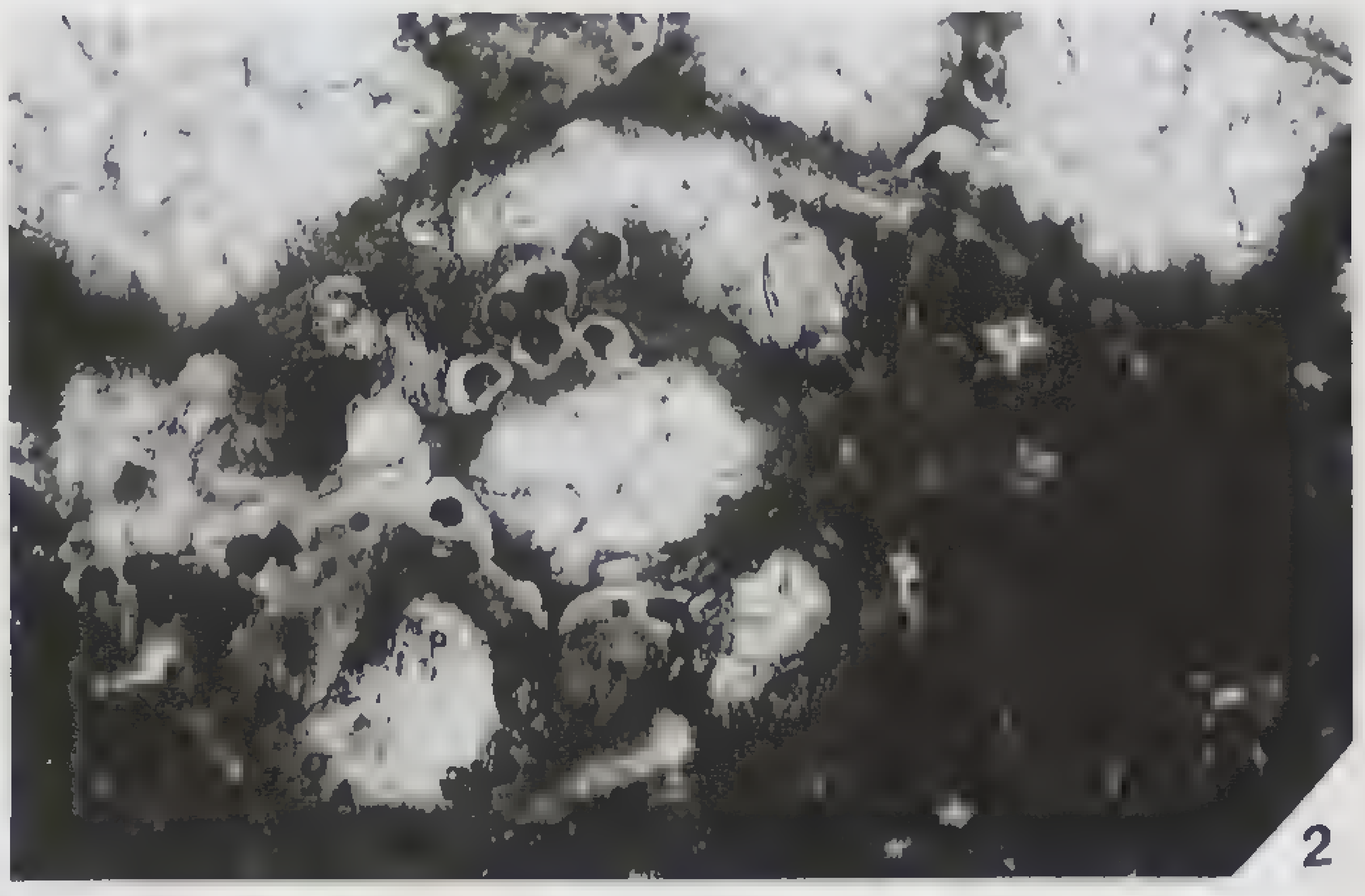
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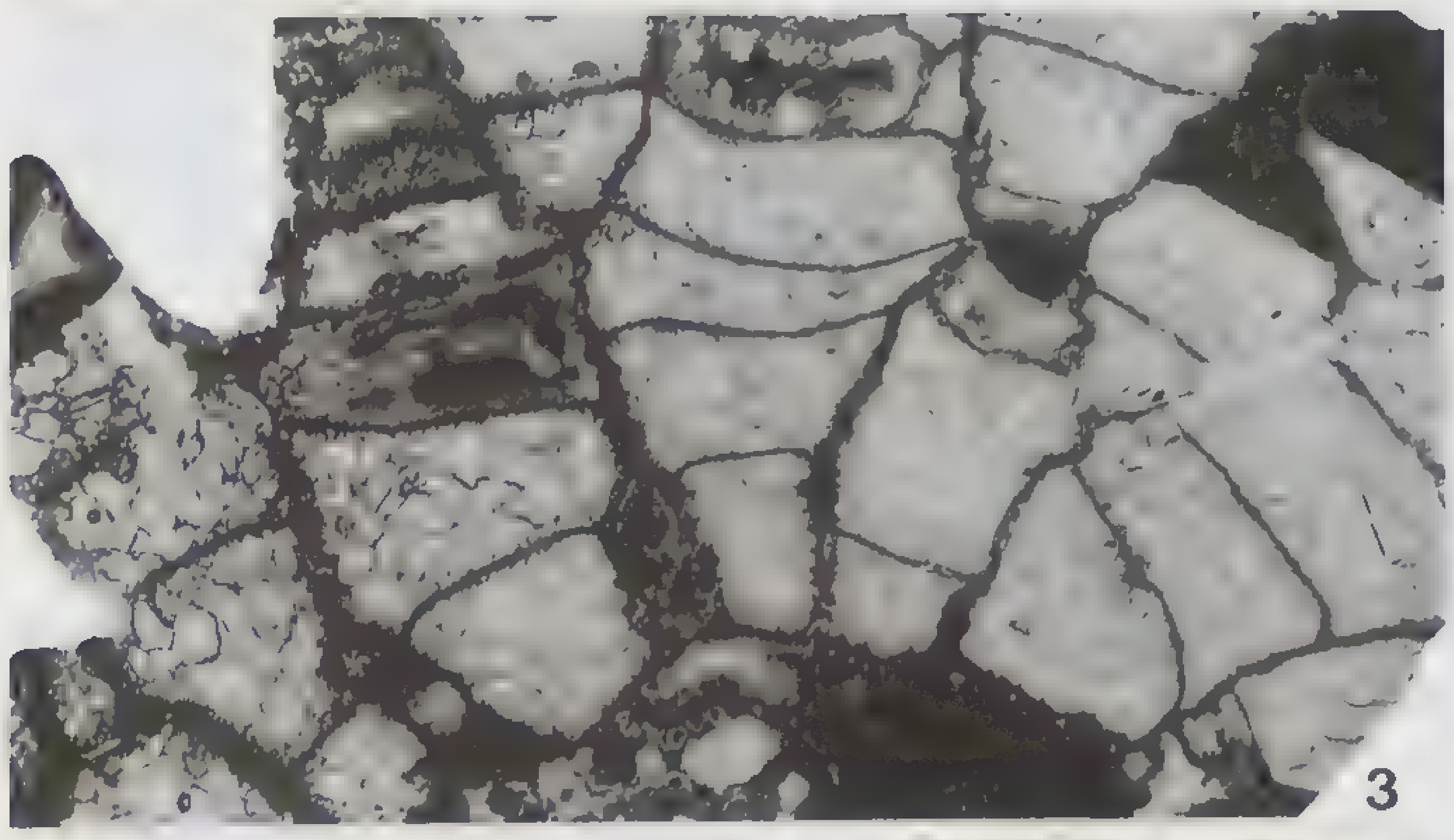
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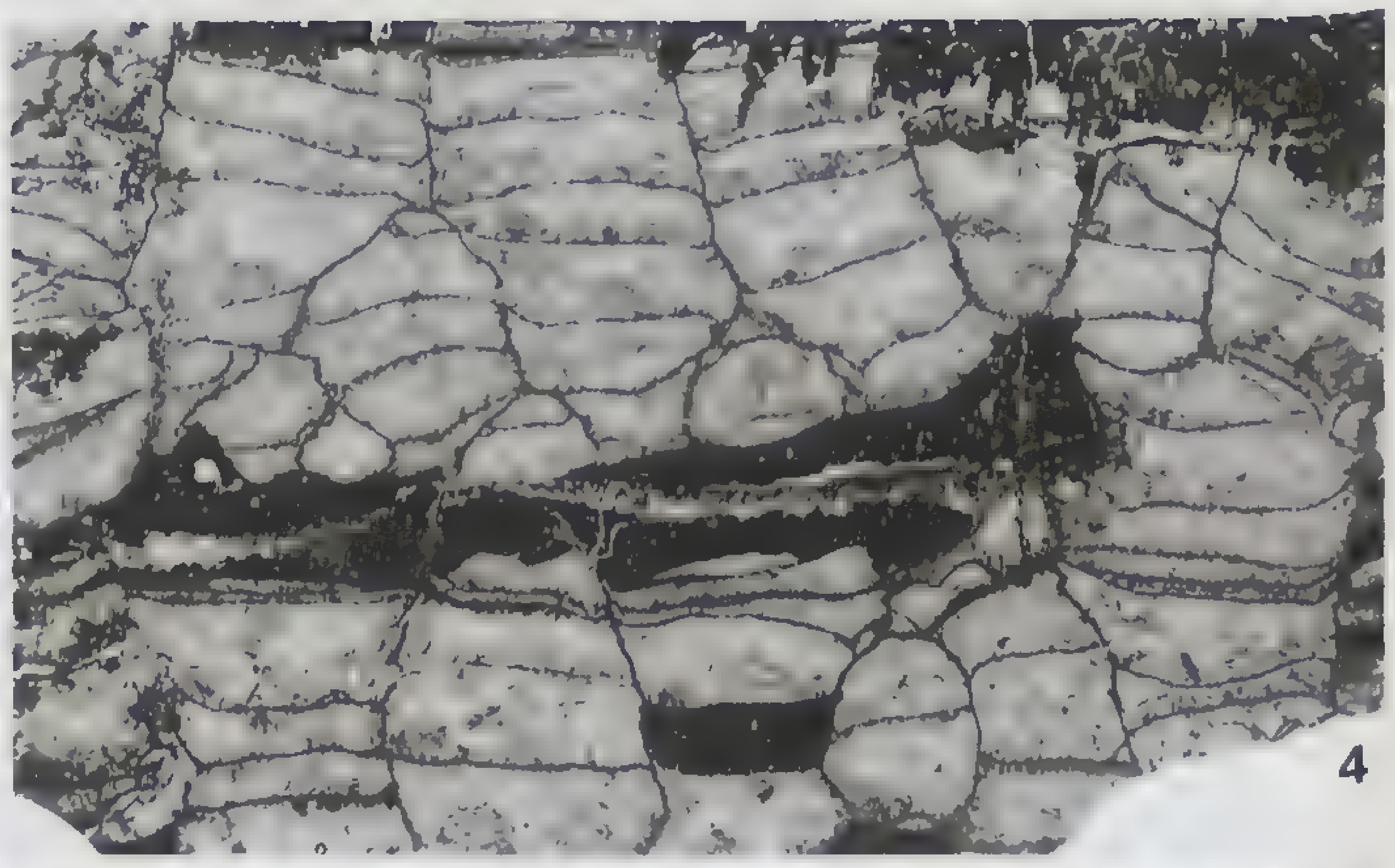
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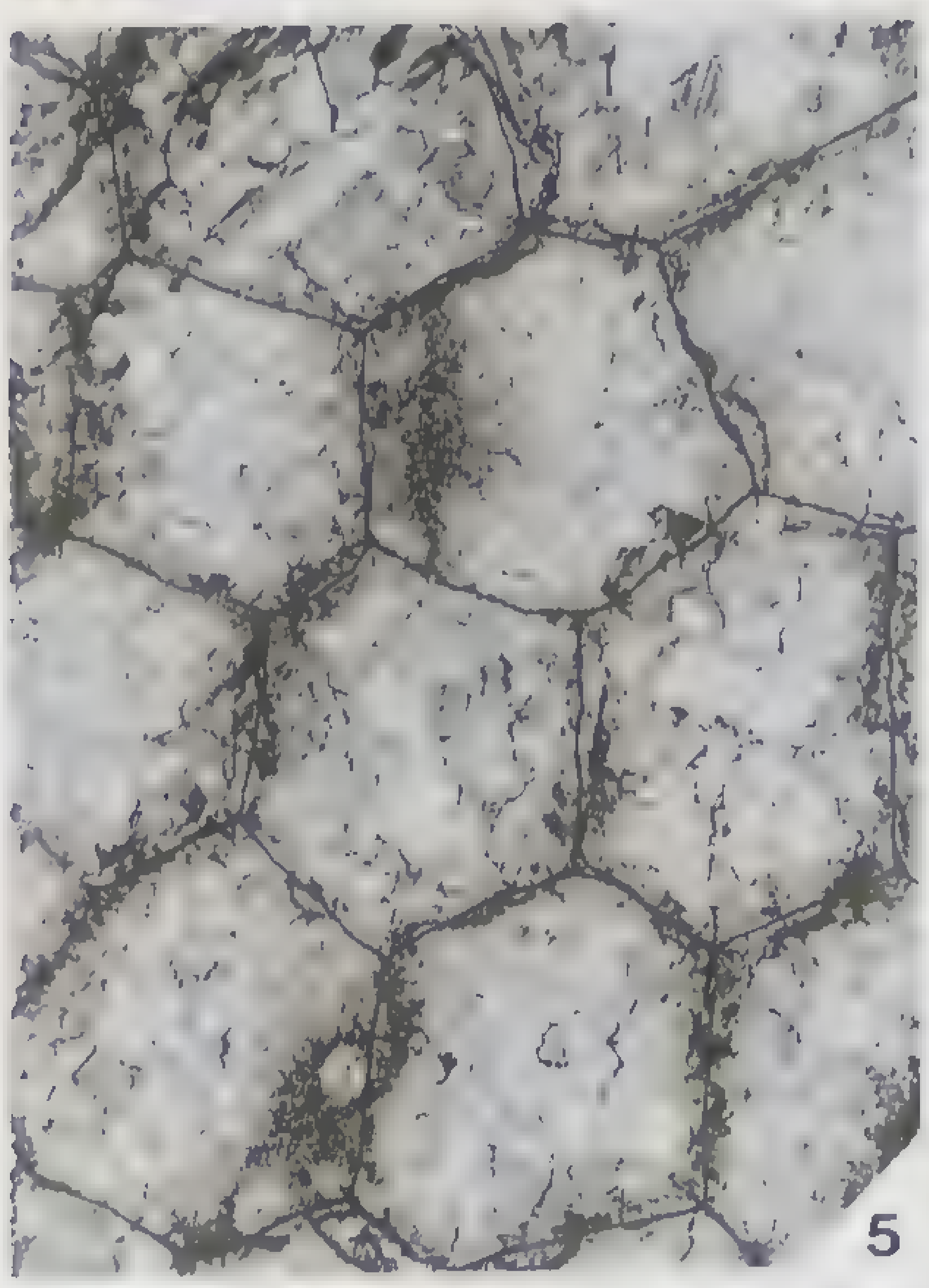
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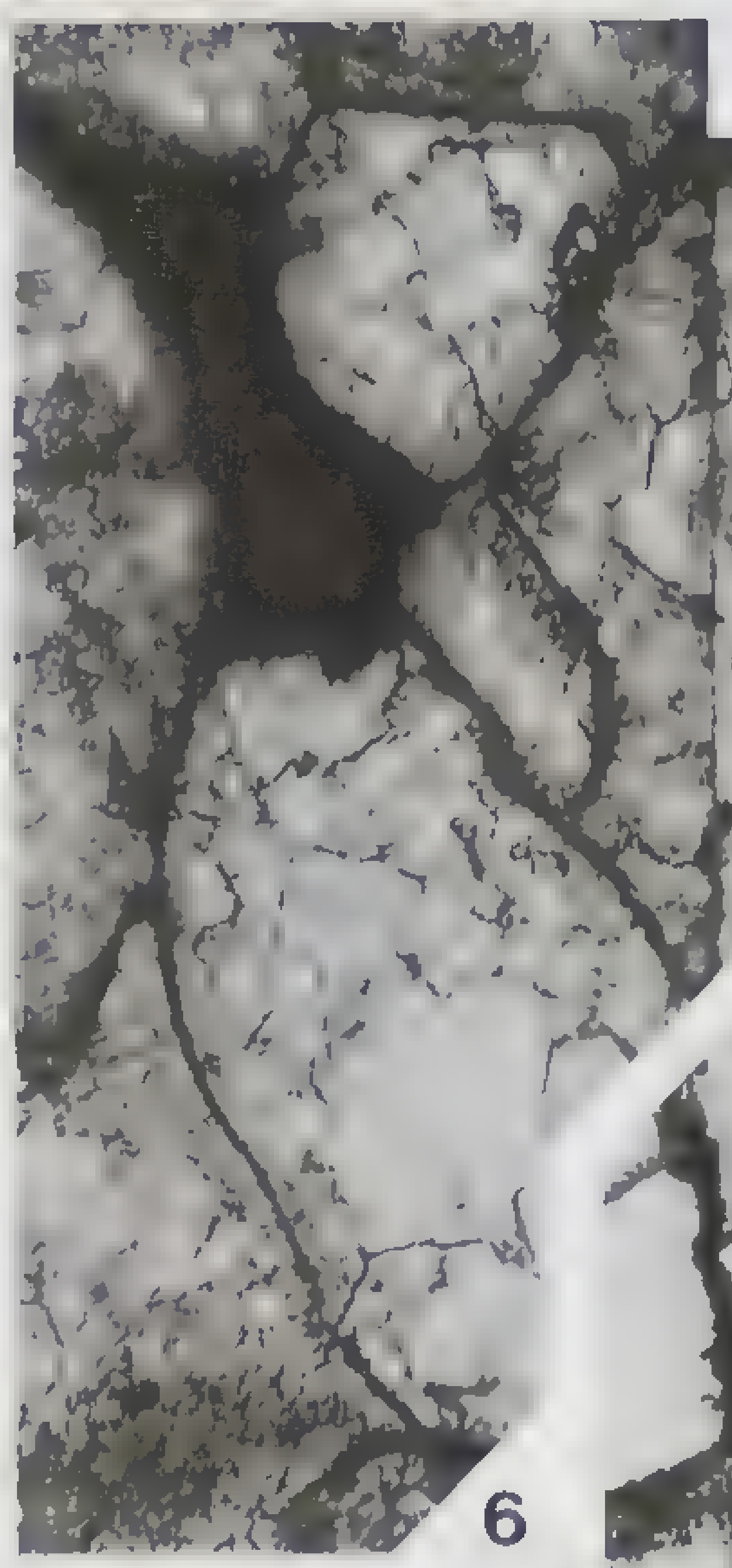
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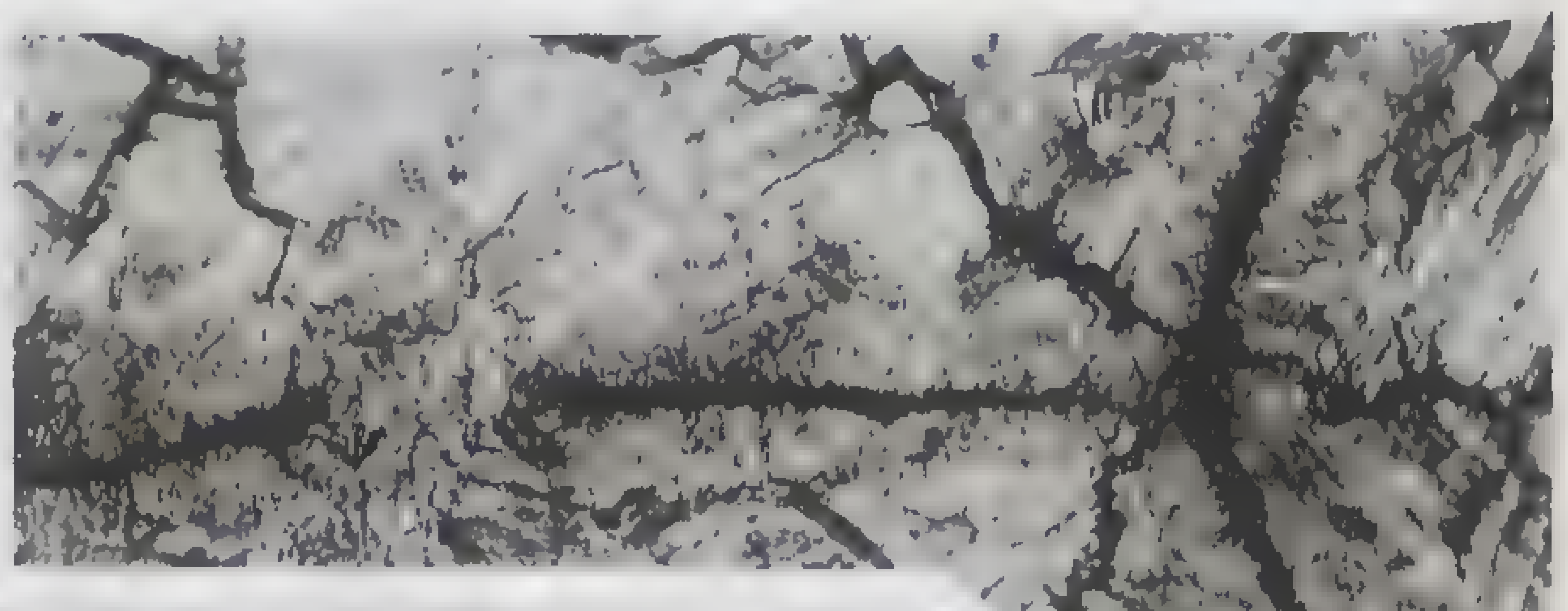
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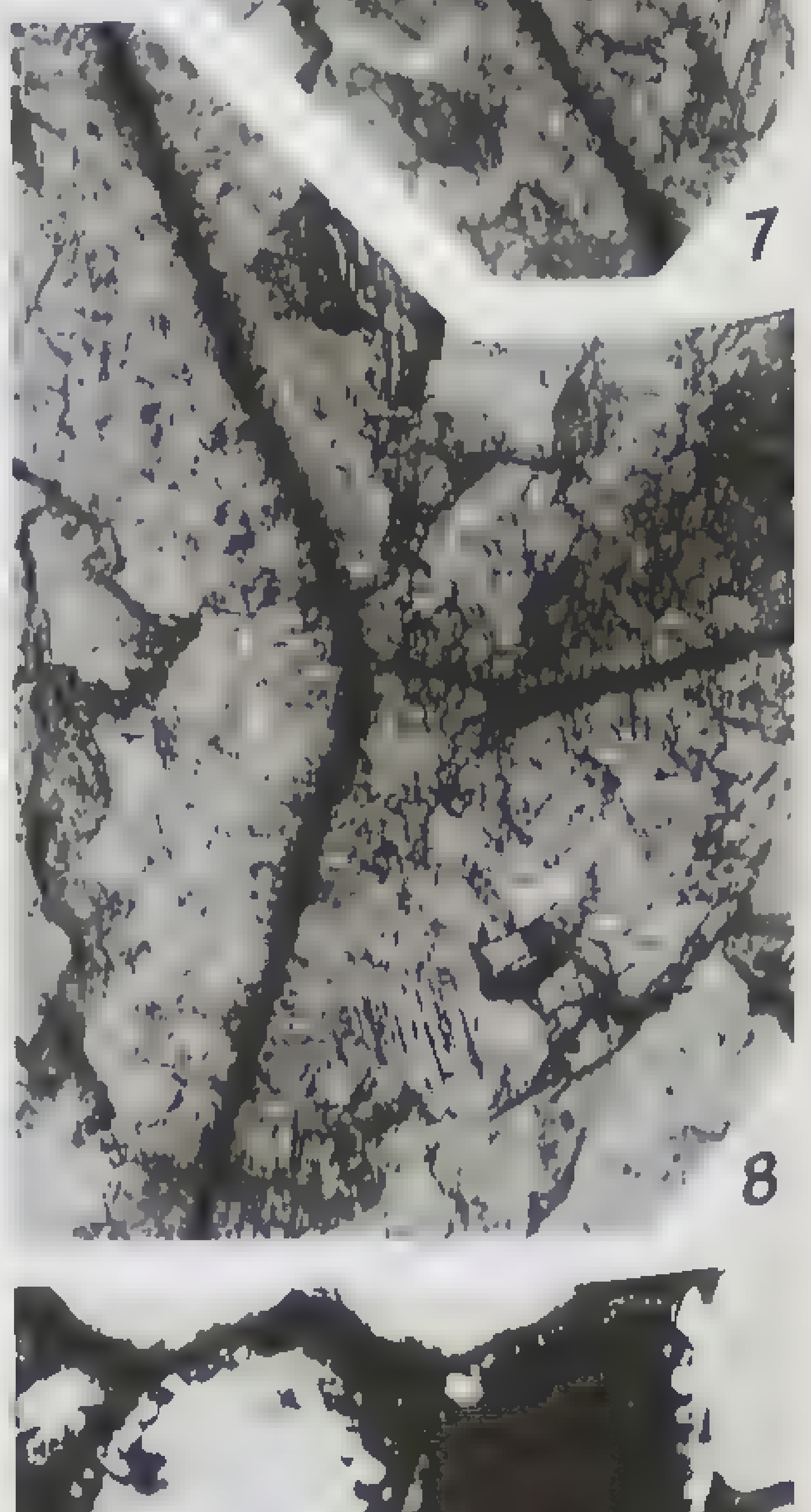
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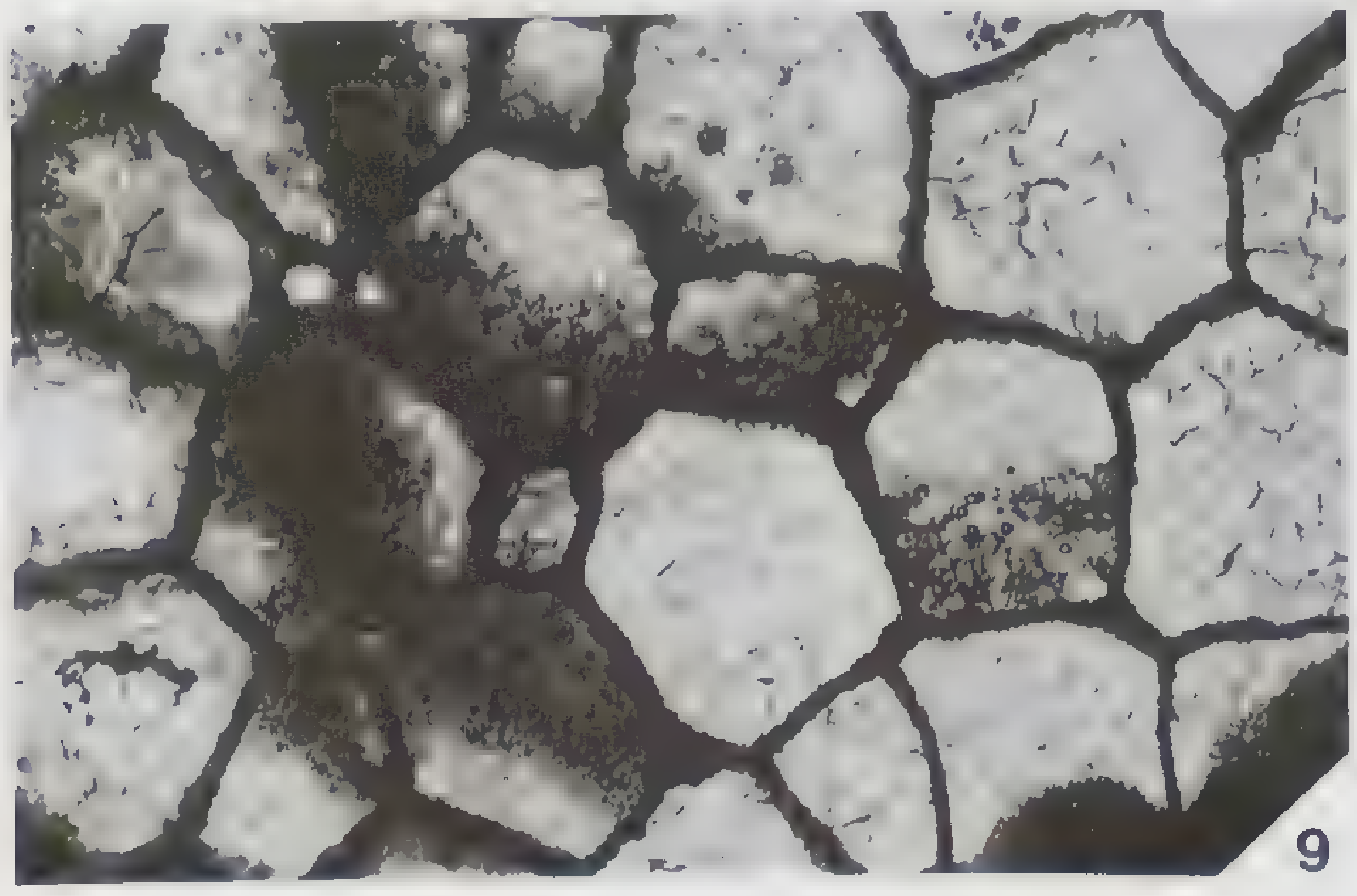
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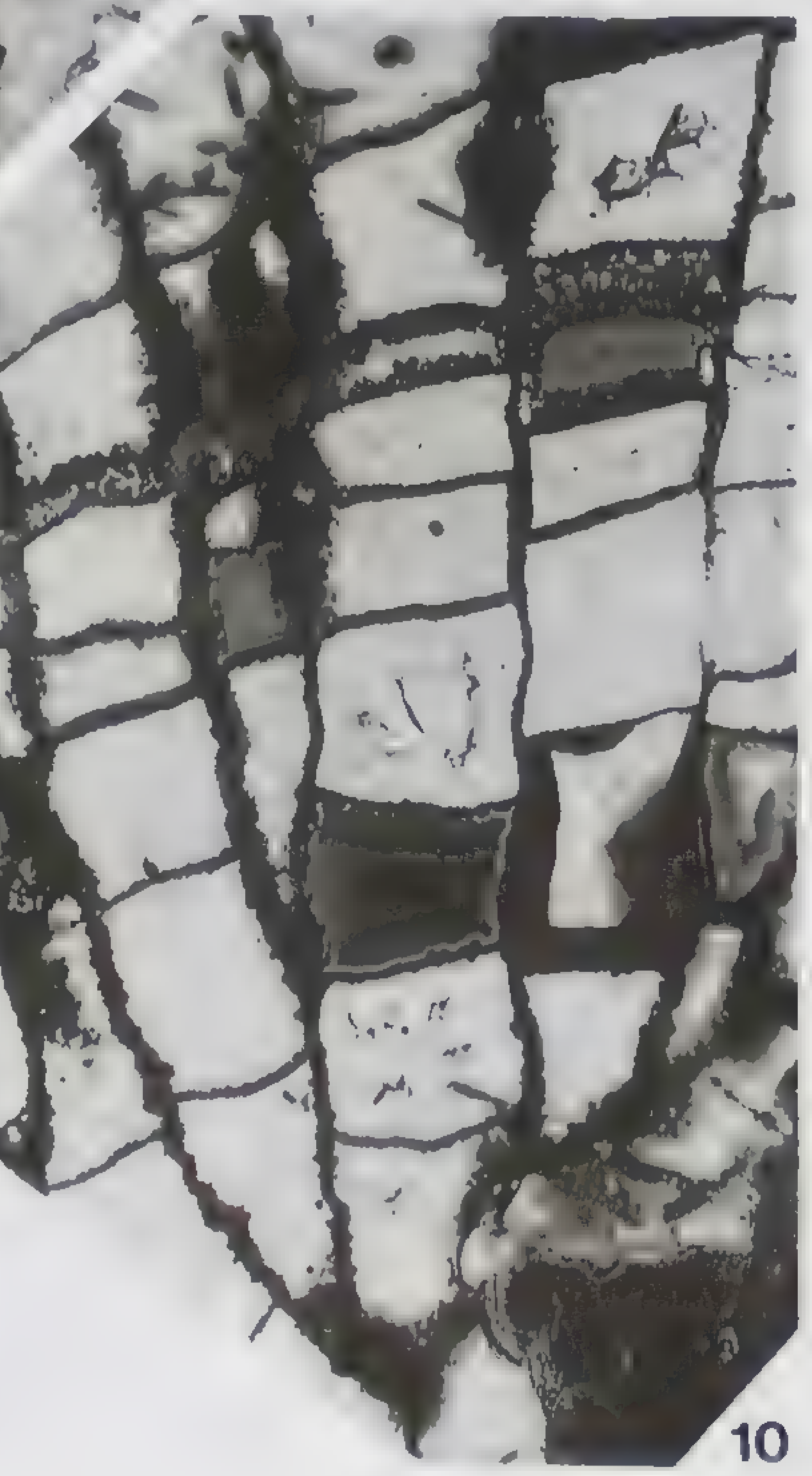
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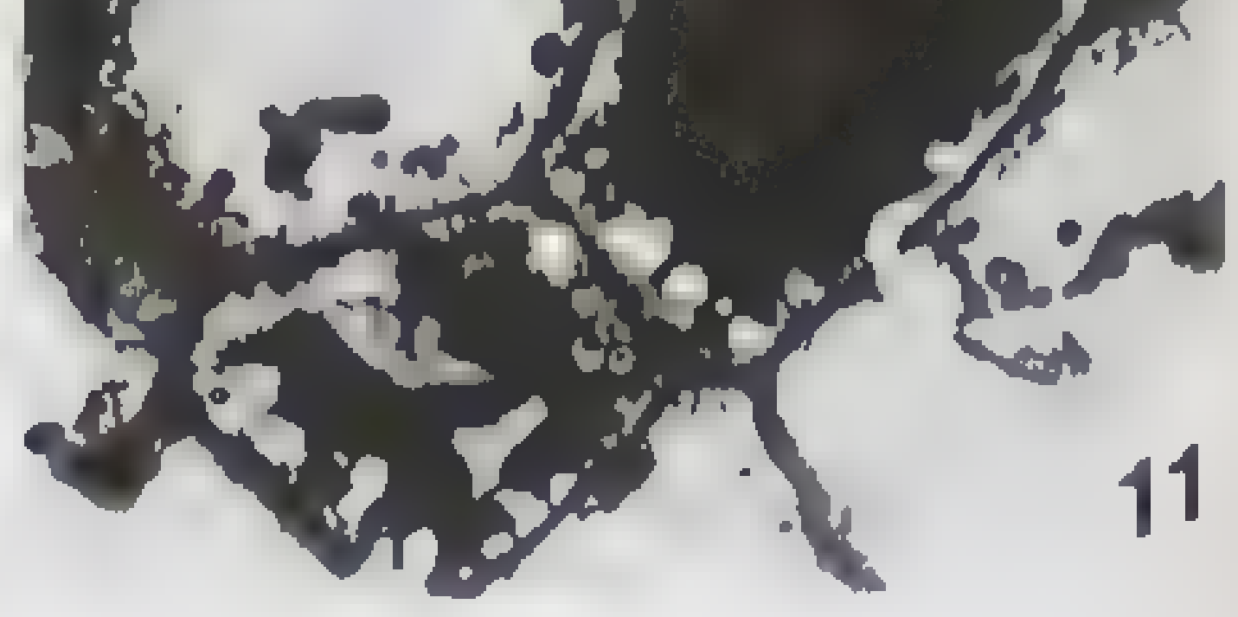
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EXPLANATION OF PLATE 18

Figure Page

1–11. ***Paleofavosites adaensis,*** new species 91

[1–3, Cochrane Formation, Section-interval 23-5 (Lawrence Quarry) (site 23i); 4–8, Cochrane Formation, Section-interval 35-1 (Henry House Falls); 9, 10, Sexton Creek Limestone, Alexander County, Illinois; 11, upper Mosalem Formation, Section-interval 10-3 (Lost Mound).]

1–3. USNM 485936 (holotype): 1, transverse section, ×5; 2, longitudinal section through base of corallum, showing group of basal corallites and holotheca, ×15; 3, longitudinal section, ×5.

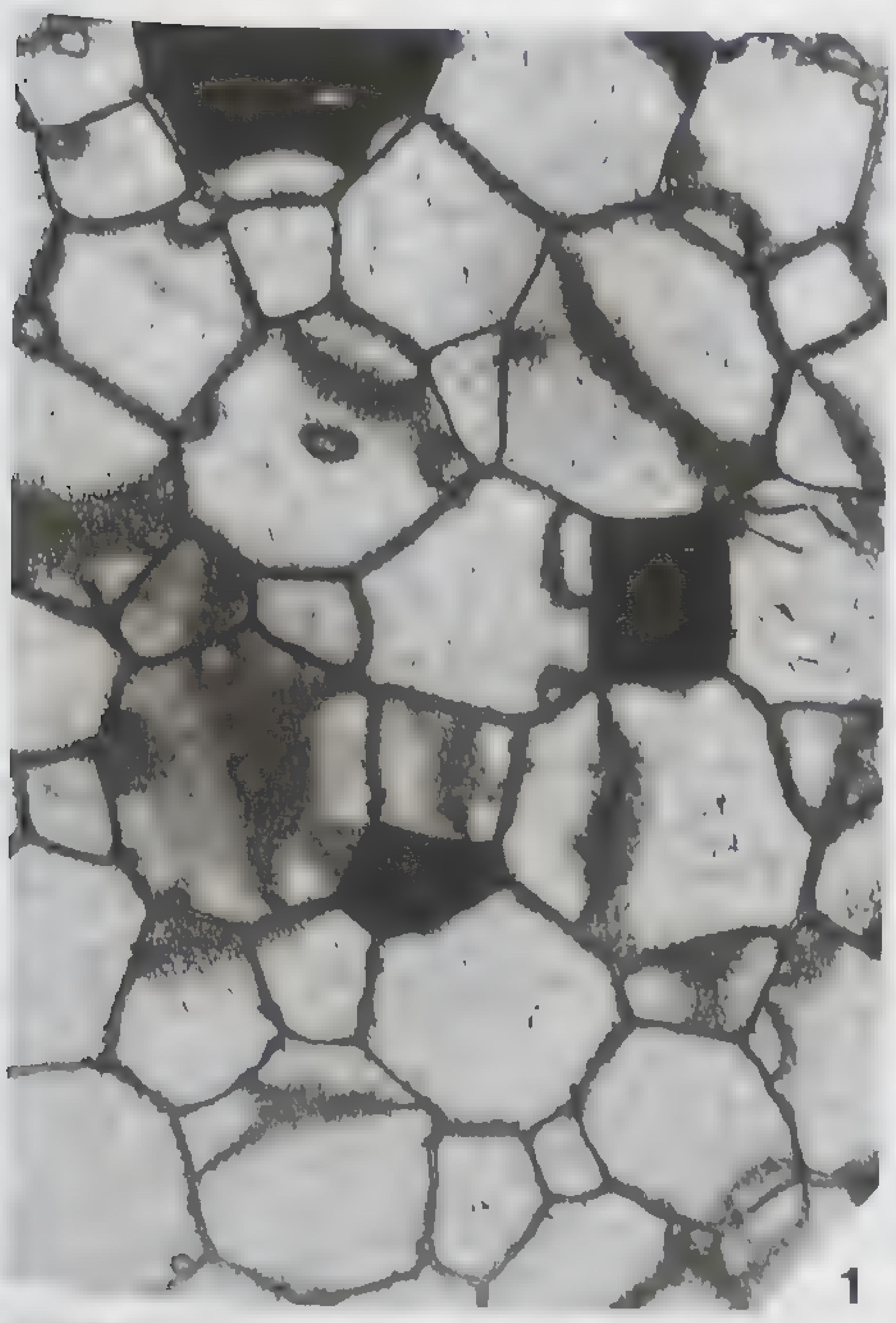
4–8. USNM 485937 (paratype): 4, longitudinal section showing sediment inclusion and regeneration, ×5; 5, transverse section, ×5; 6, transverse section showing offsets produced during regeneration, ×15; 7, transverse section showing walls and mid-wall pore, ×40; 8, transverse section showing walls and corner pore, ×40.

9, 10. UI C-1347: 9, transverse section, ×5; 10, longitudinal section, ×5.

11. USNM 485941: transverse section, ×5.

EXPLANATION OF PLATE 19

Figure		Page
1–7.	***Paleofavosites*** species cf. ***P. ivanovi*** Sokolov, 1951a	94
	[1–5, limestone facies at base of Bowling Green Dolomite, Section-interval 17-1a (Clarksville); 6, 7, Bowling Green Dolomite, Section-interval 36-1 (Indian Creek).]	
	1–5. USNM 485943: 1, transverse section, ×5; 2, transverse section of corallites at corallum margin, showing wall structure and curved free walls, ×20; 3, longitudinal section (note axial depressions in tabulae), ×8; 4, transverse section (detail from left of center in 1, turned 80° clockwise), ×8; 5, transverse section showing wall structure, ×40.	
	6, 7. USNM 485942: 6, longitudinal section, ×5; 7, transverse section, ×8.	
8–12.	***Paleofavosites*** species A	96
	[8, Elwood Formation, Section-interval 5-2 (Schweizer North); 9–12, Elwood Formation, Section-interval 6-1 (Plaines West).]	
	8. USNM 485944: exterior view of transverse surface (note crenulate tabulae), ×5.	
	9, 10. USNM 485948: 9, transverse section, ×8; 10, longitudinal section, ×8.	
	11, 12. USNM 485946: 11, transverse section, ×8; 12, longitudinal section showing cyclomorphic variation in spacing of tabulae, ×8.	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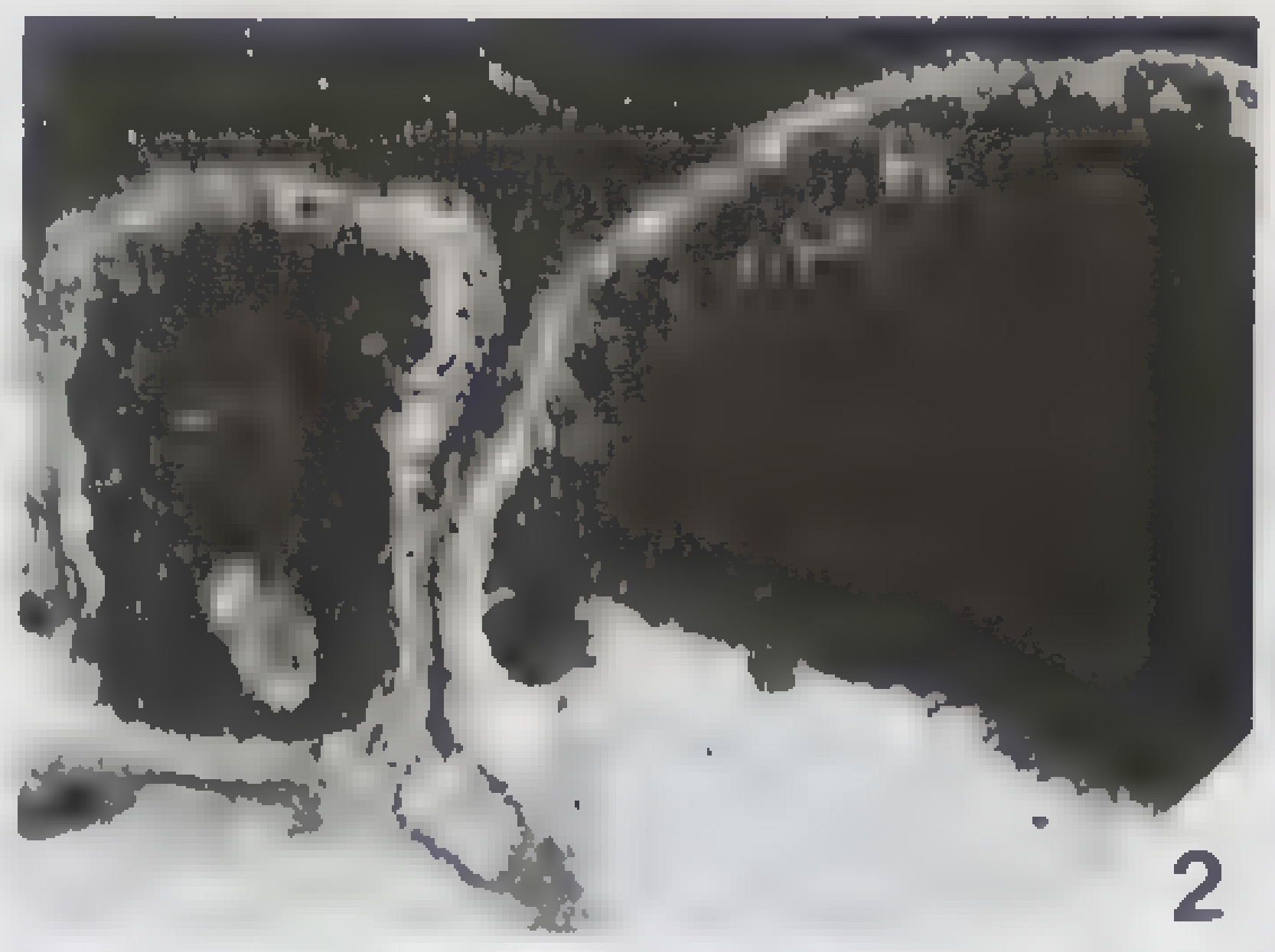
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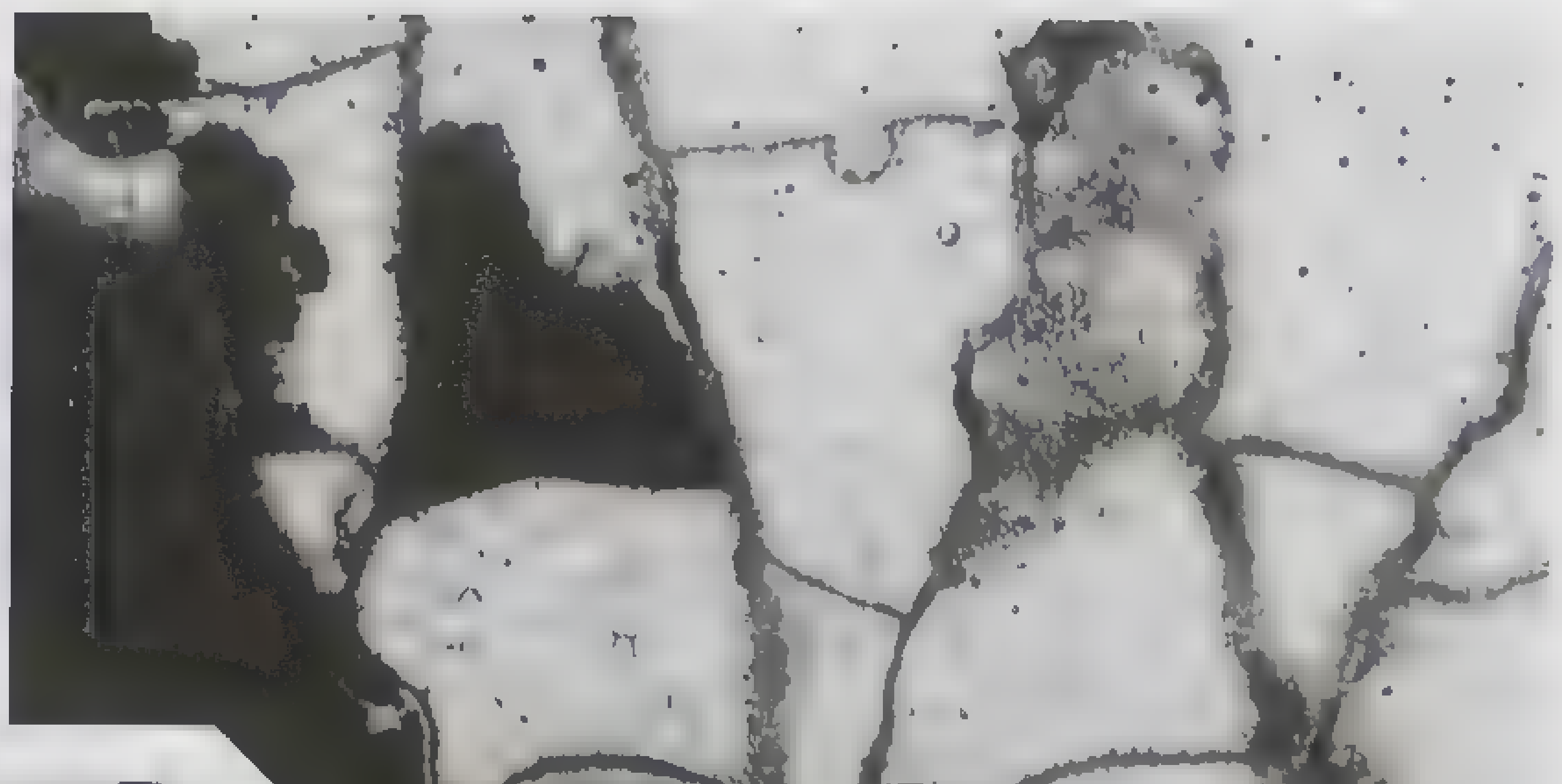
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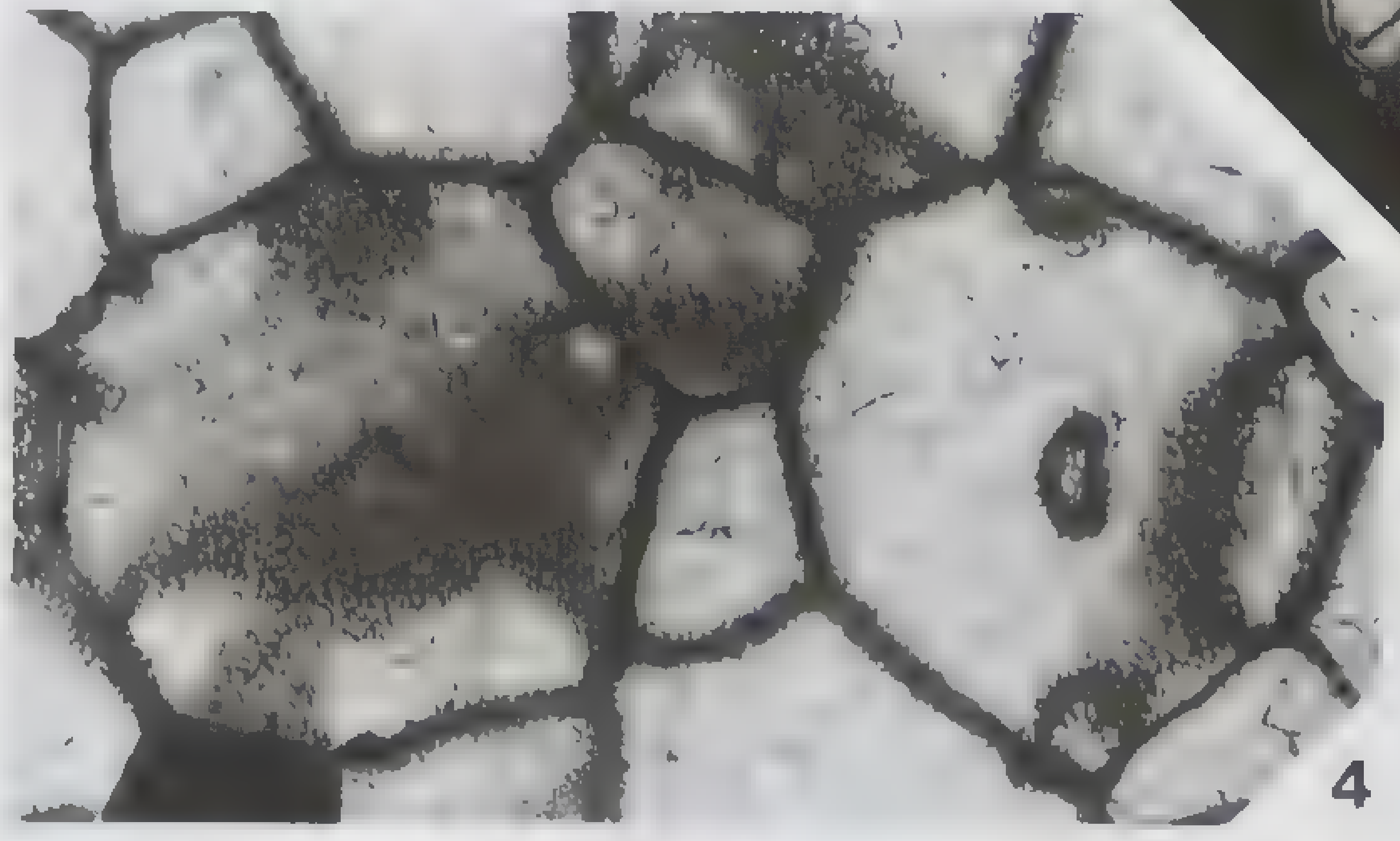
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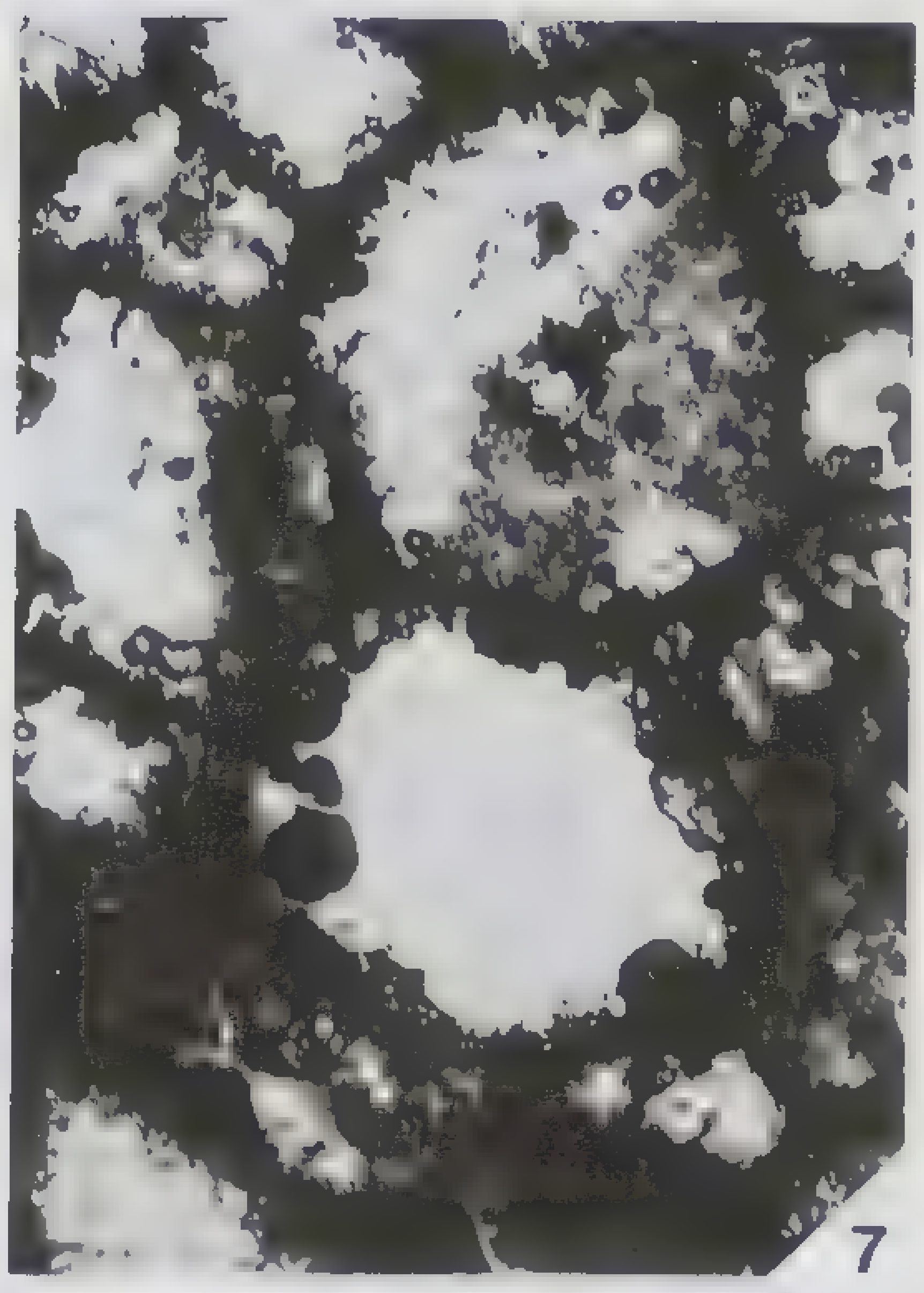
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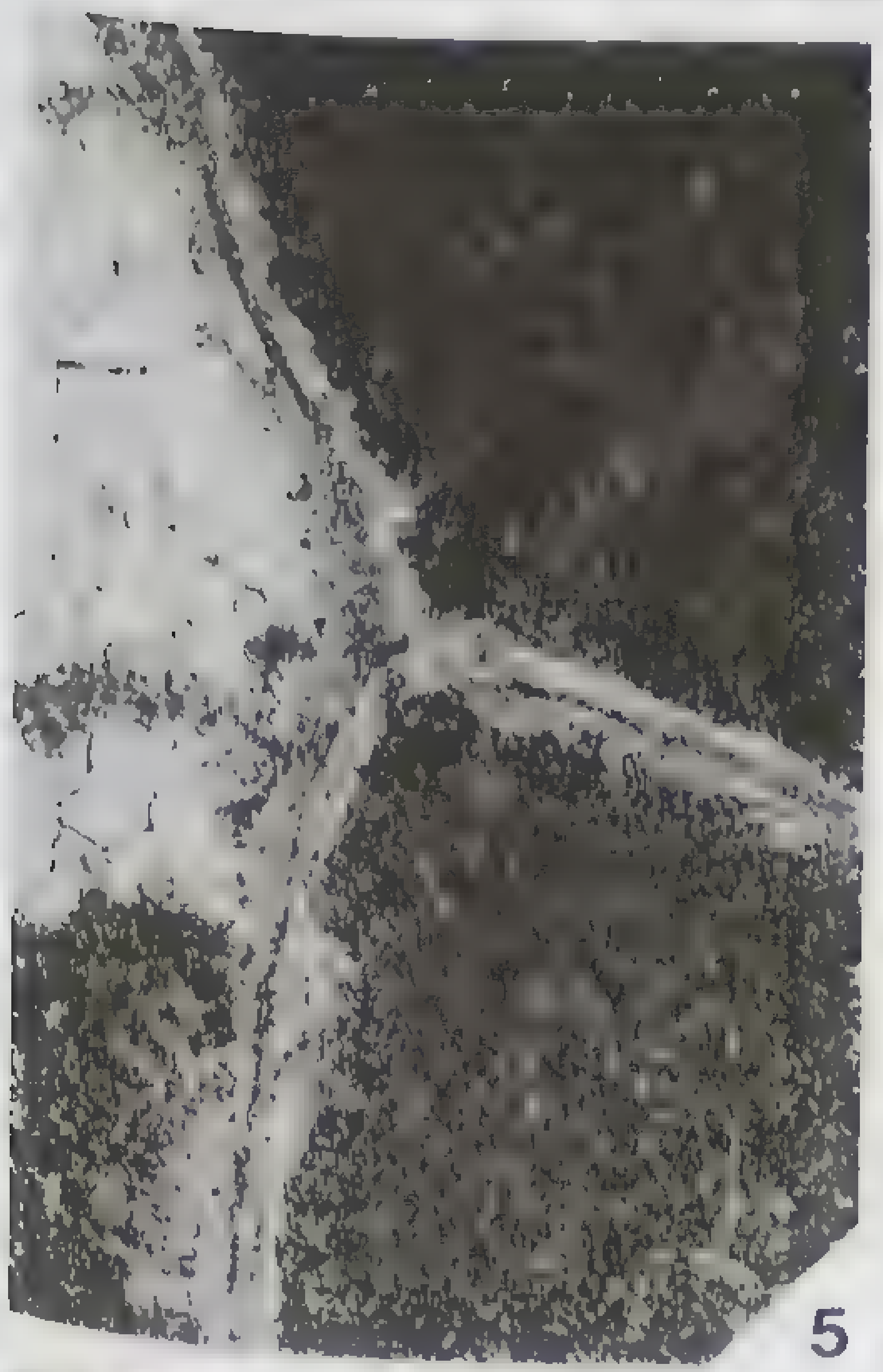
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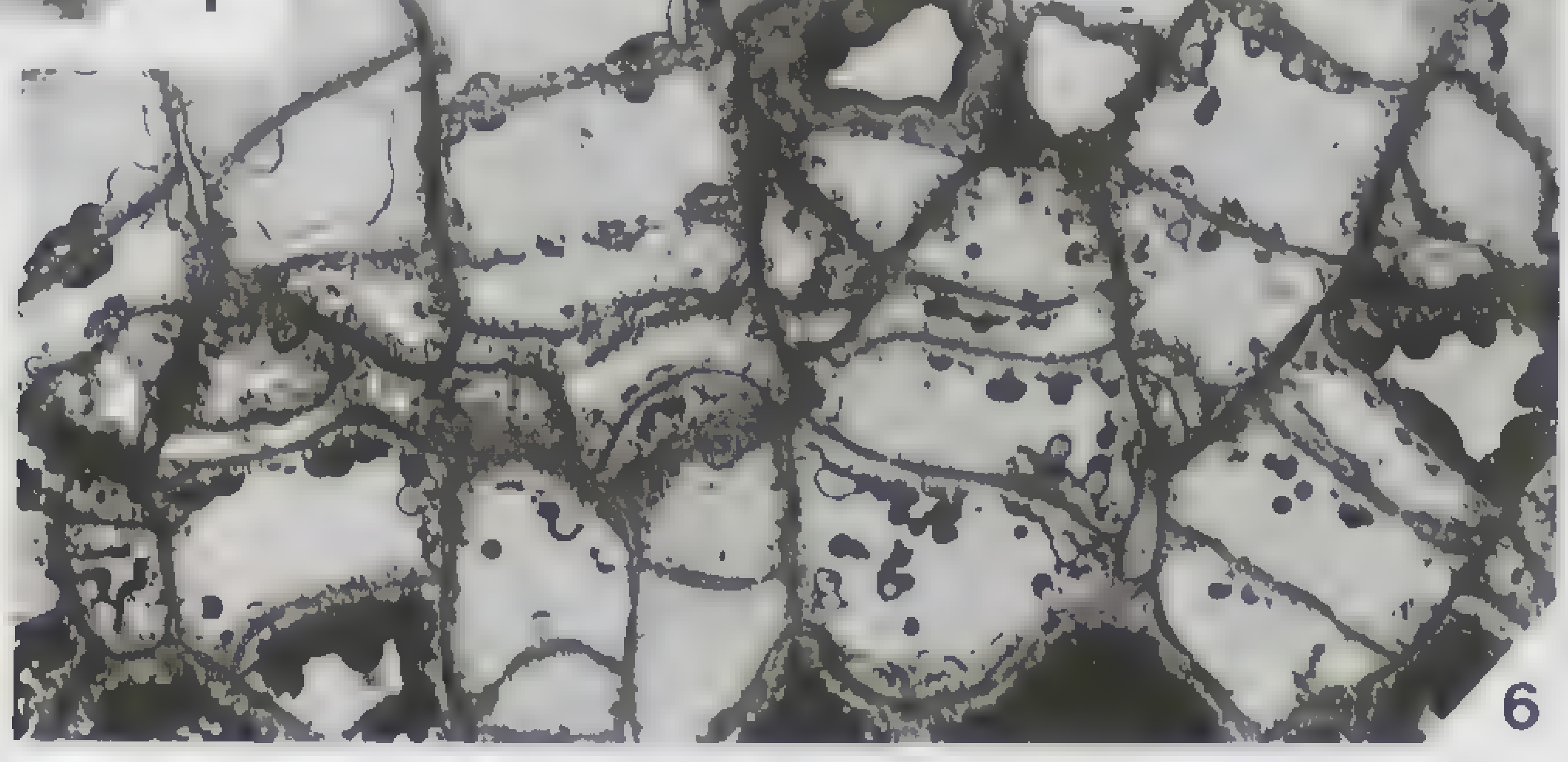
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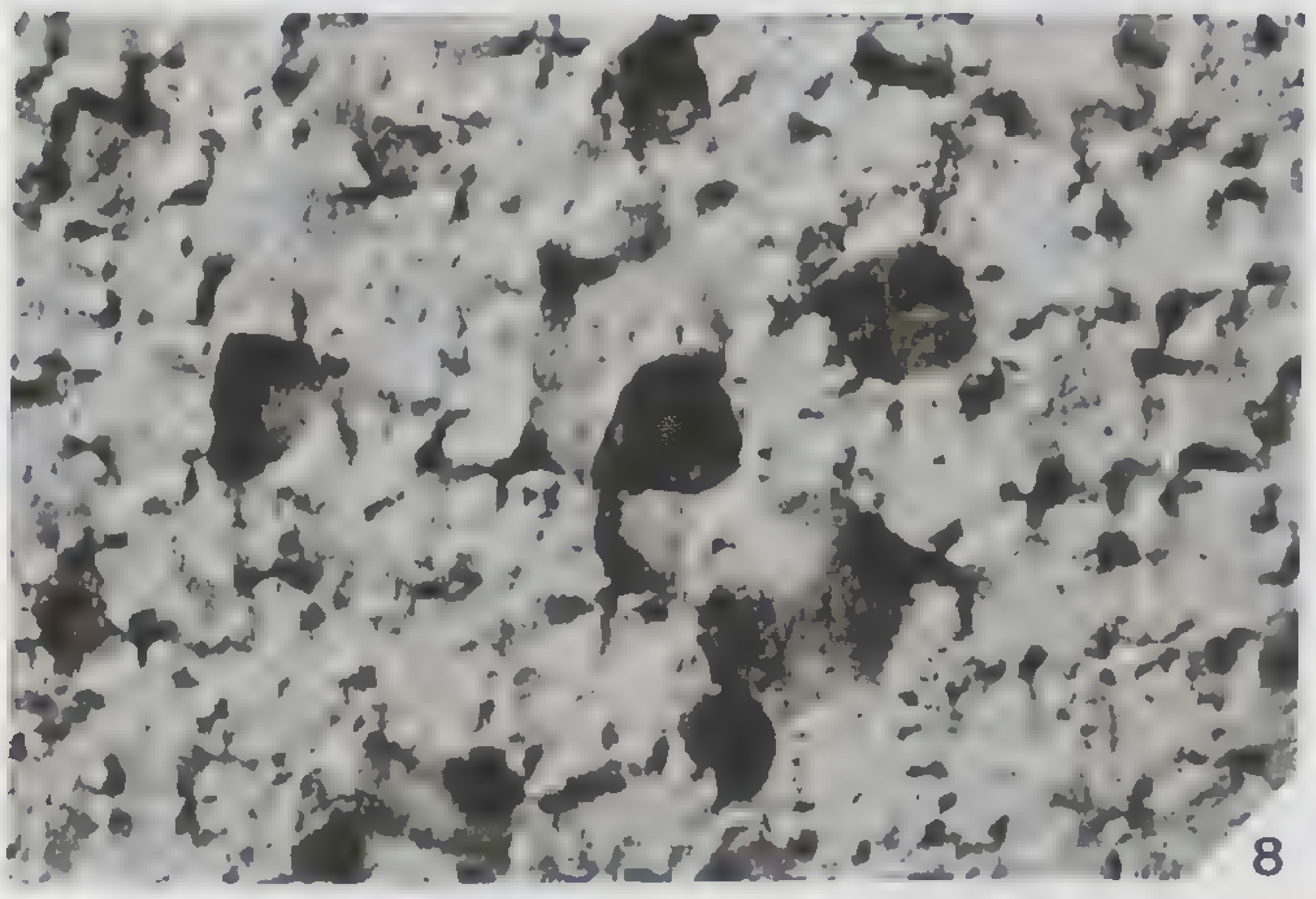
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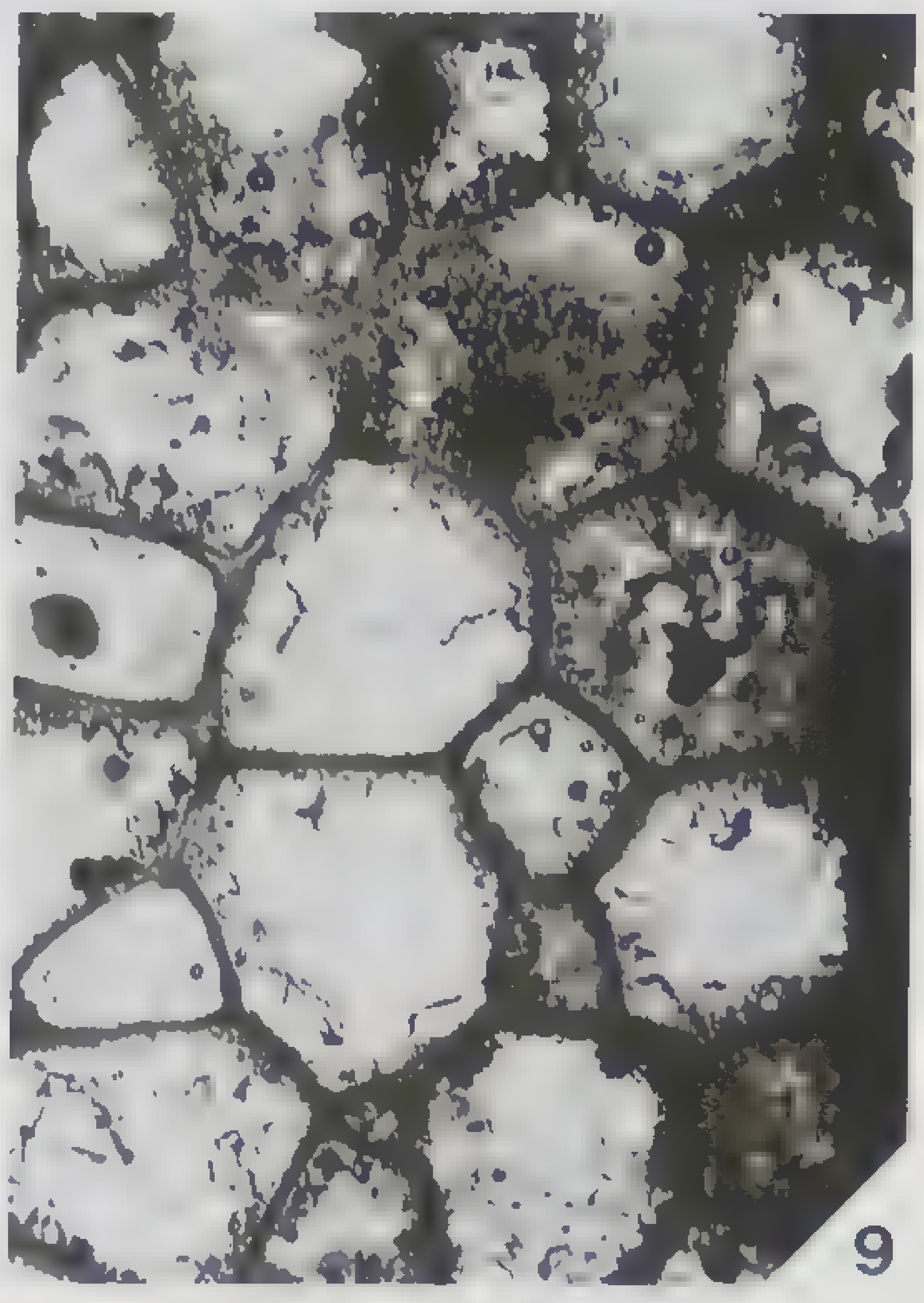
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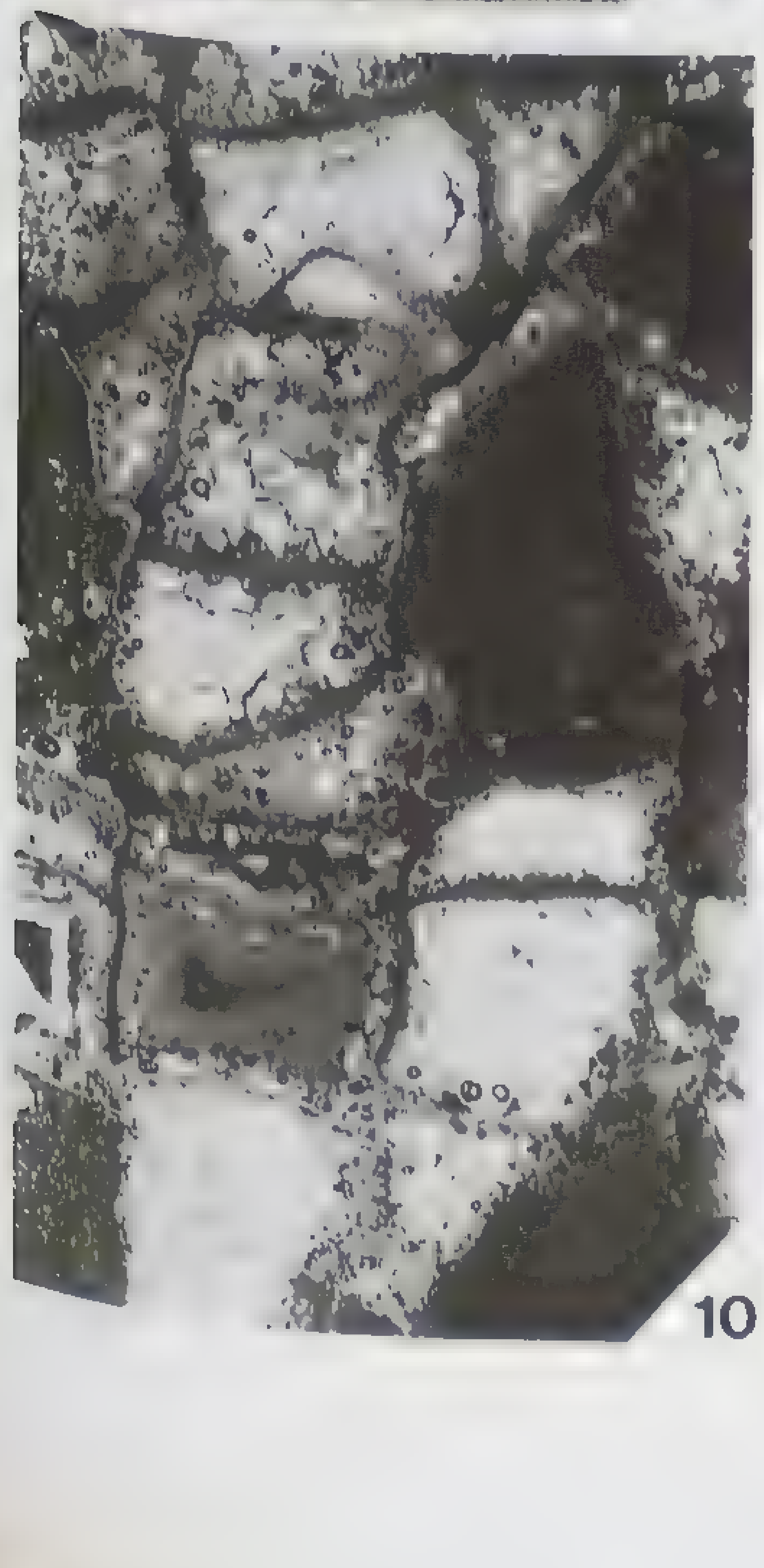
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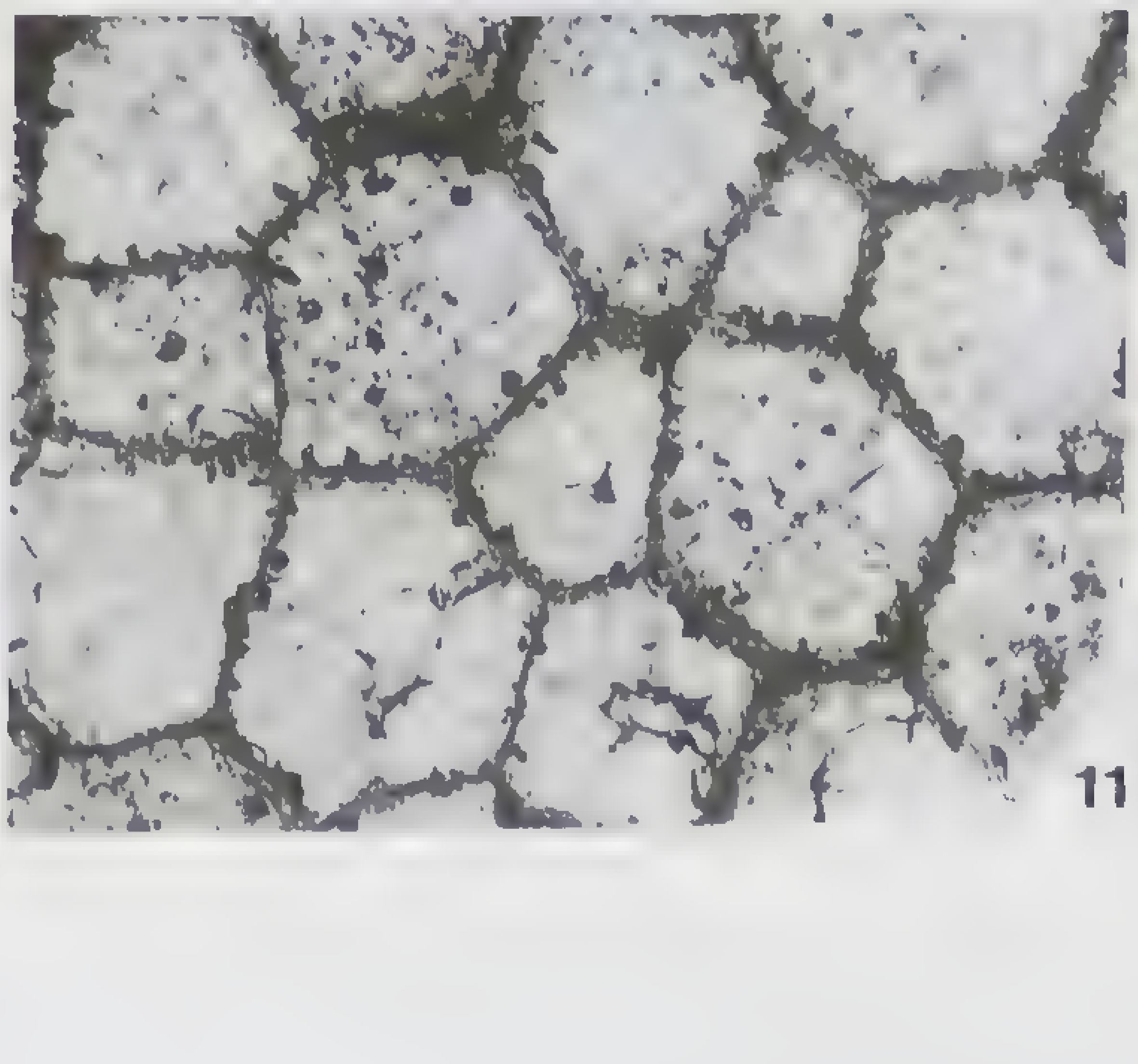
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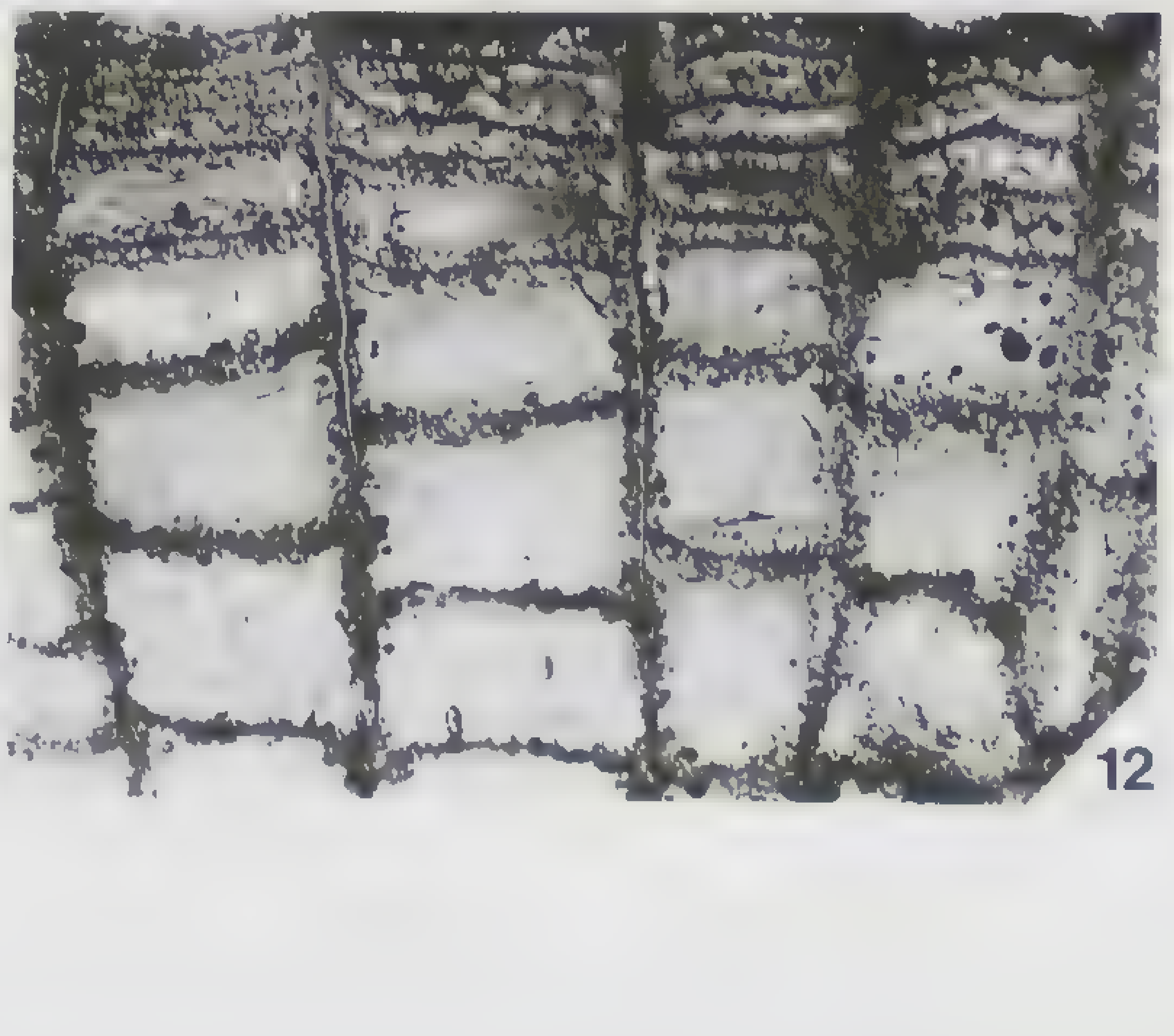
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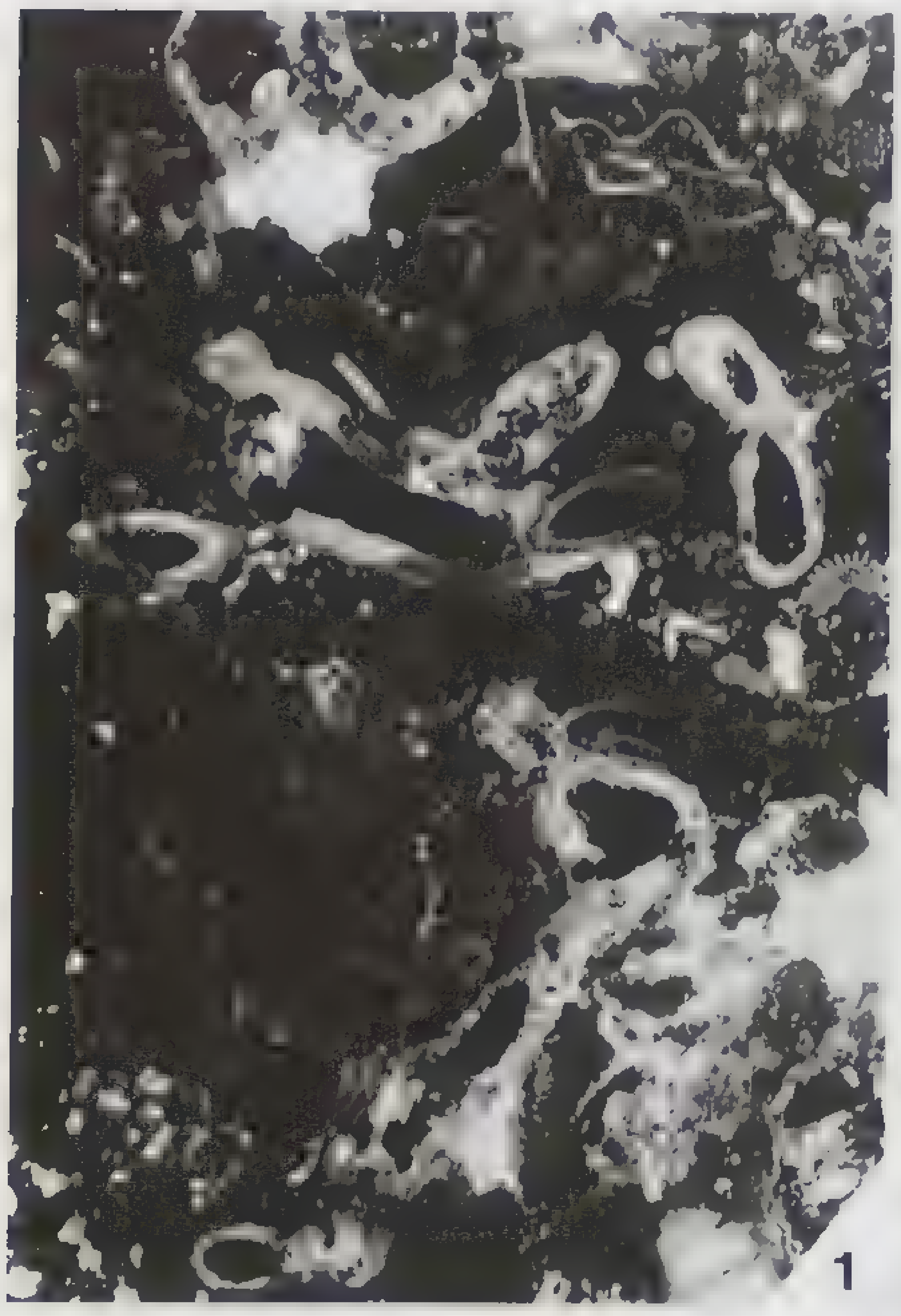
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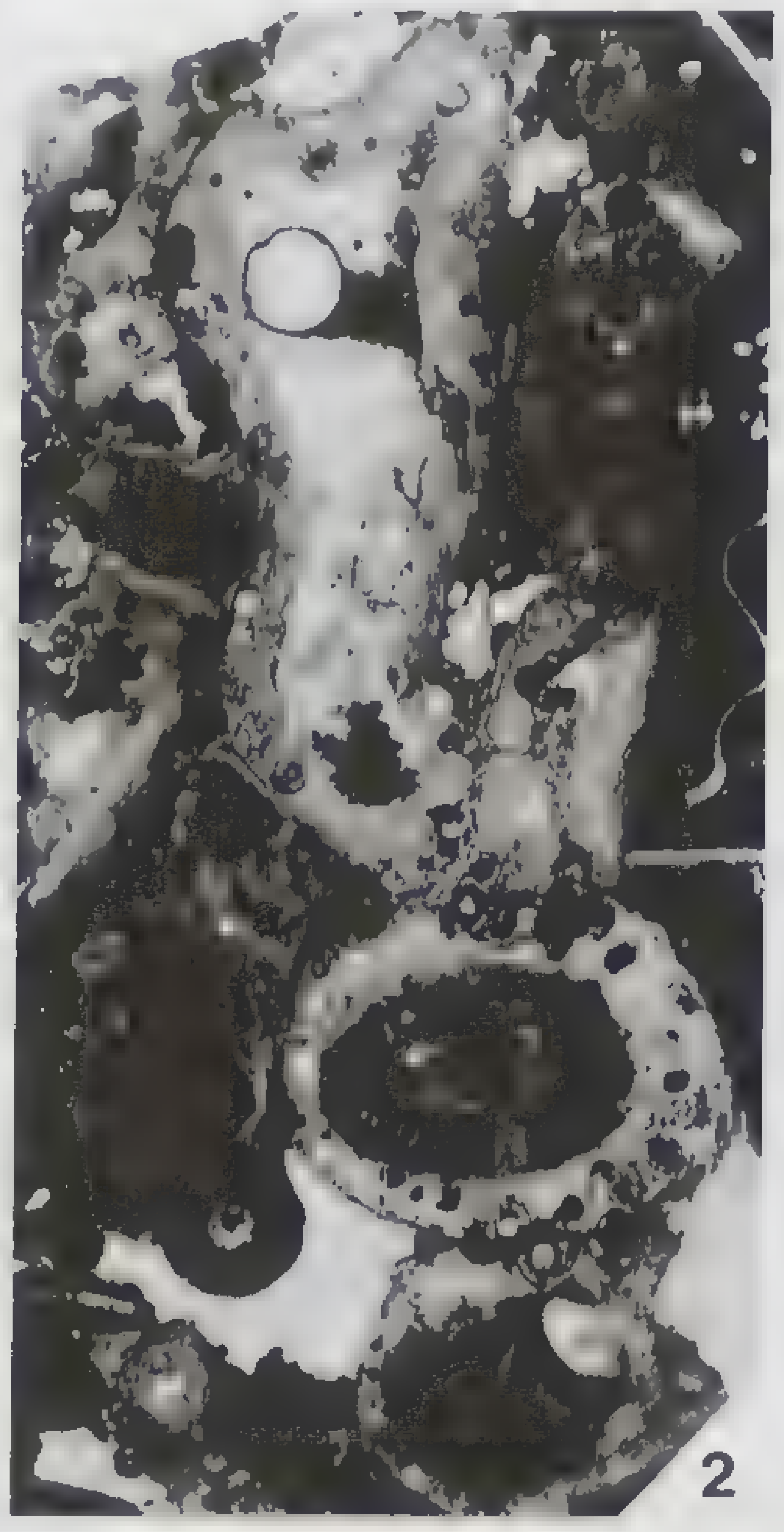
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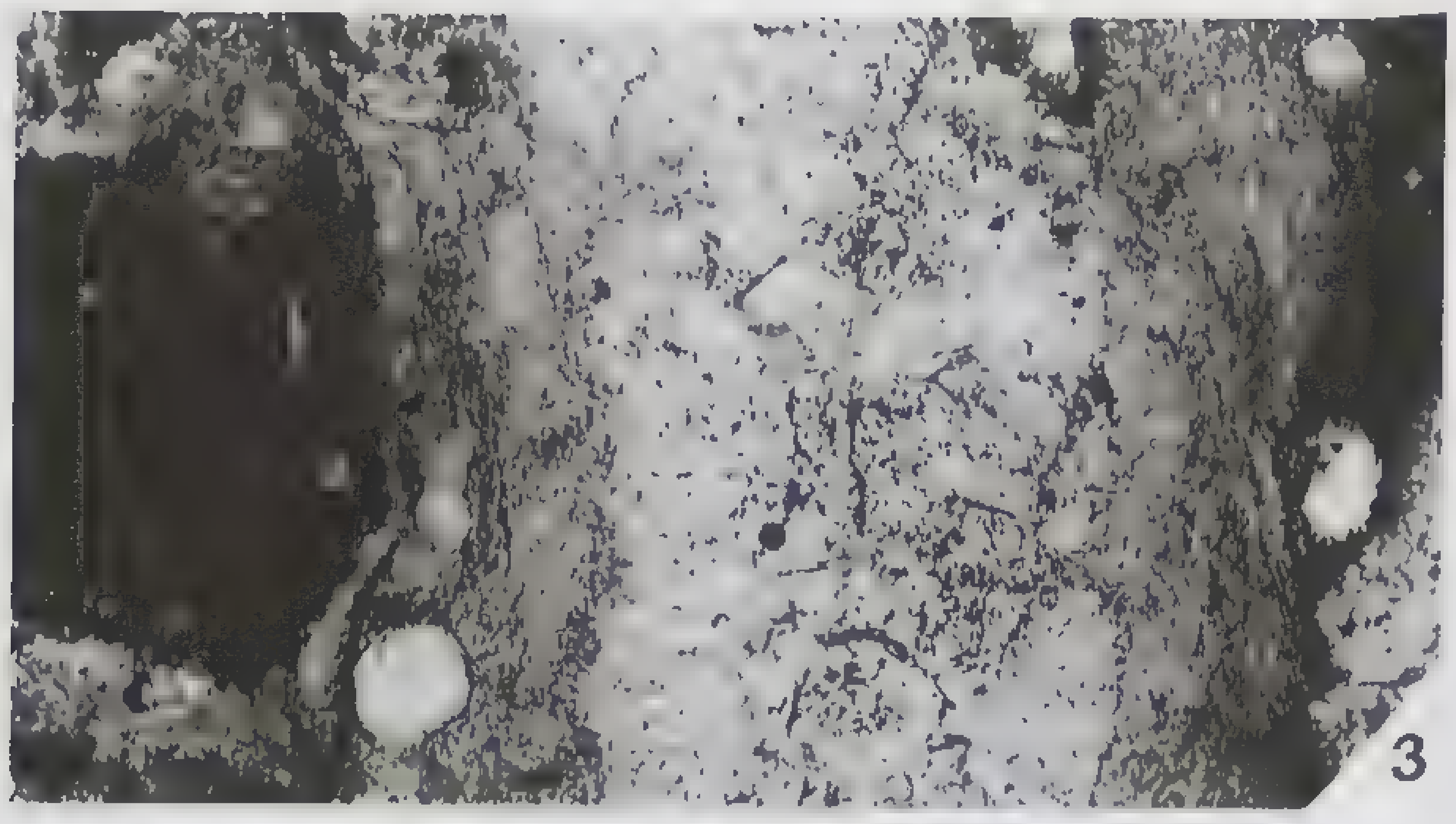
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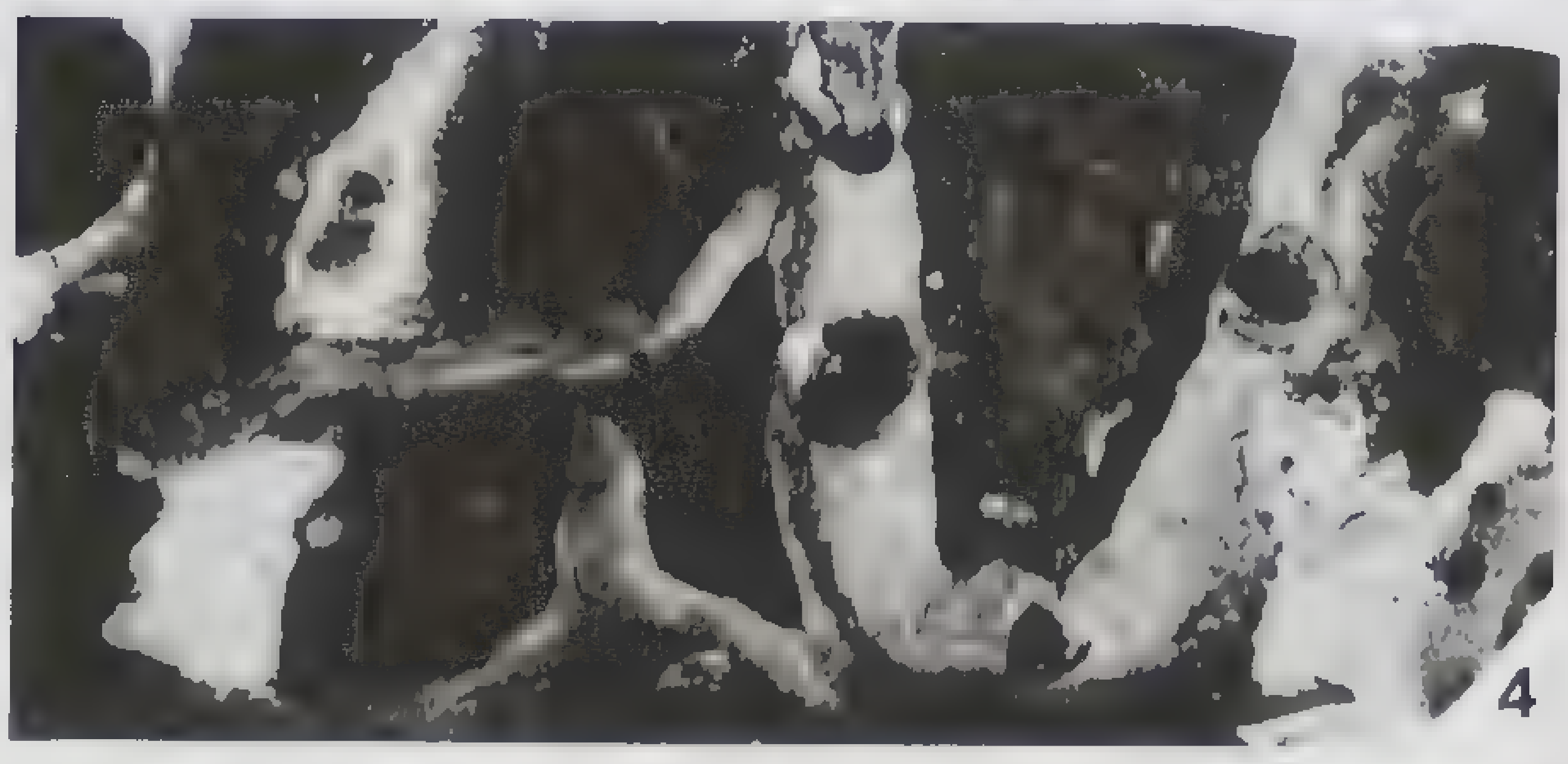
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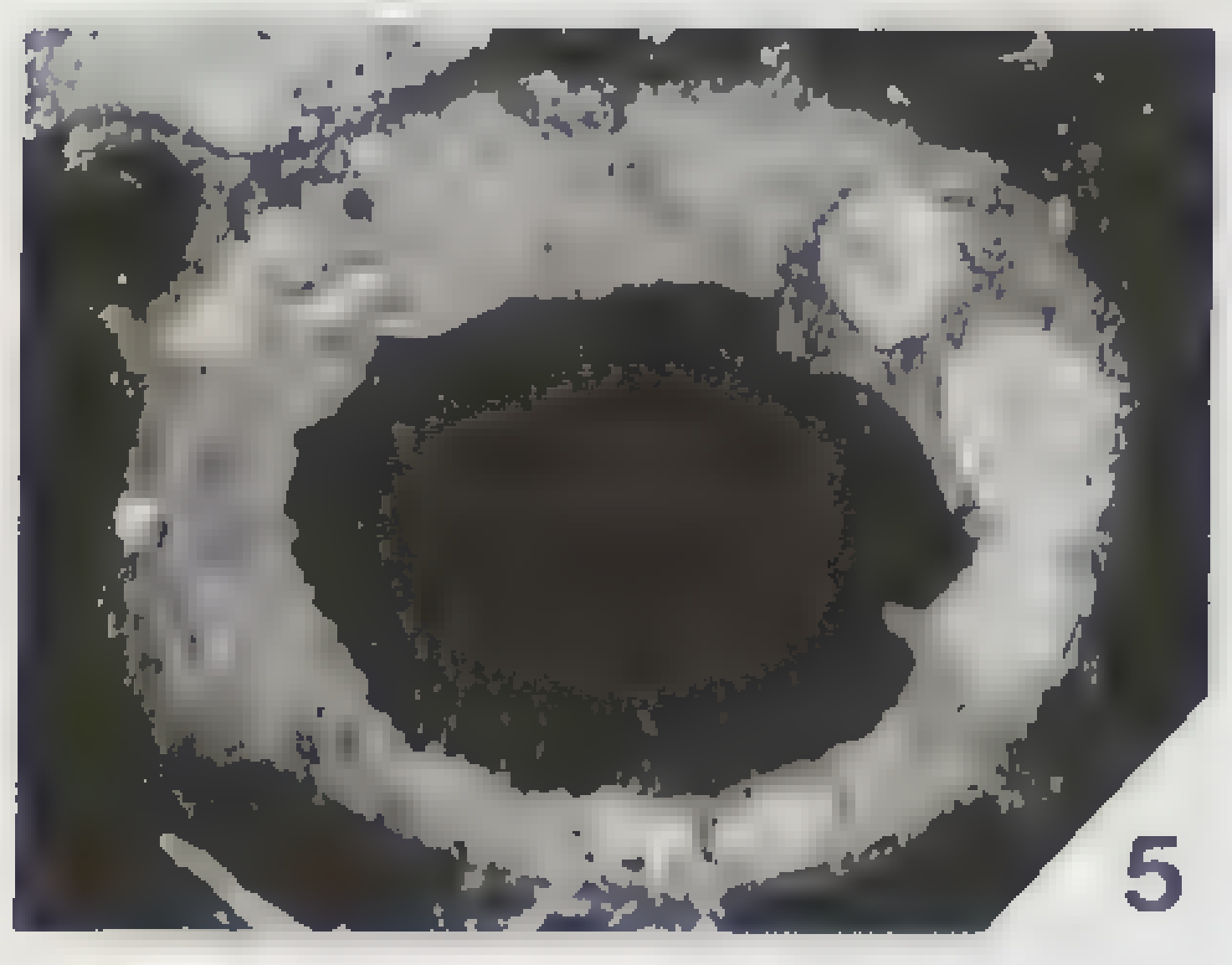
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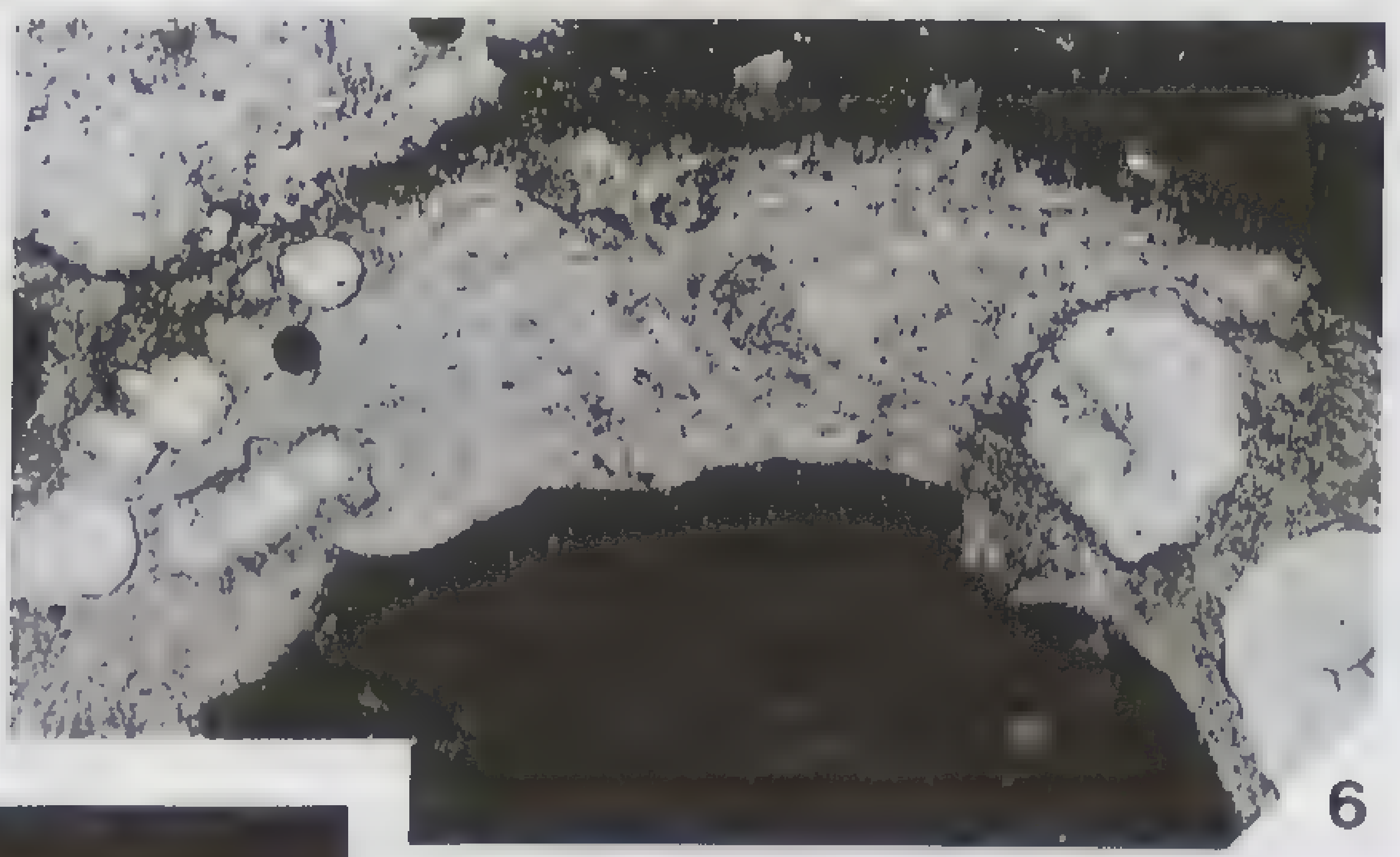
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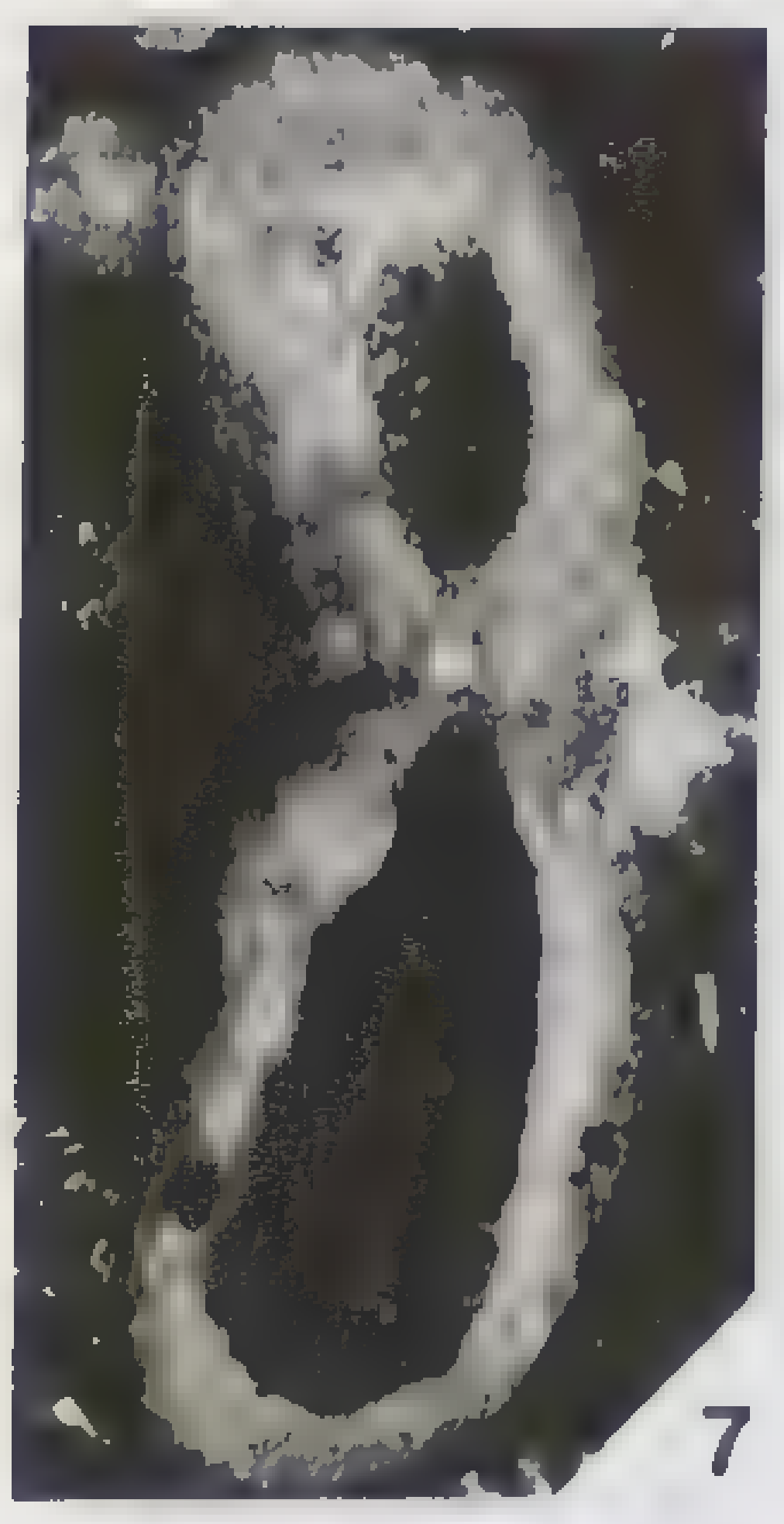
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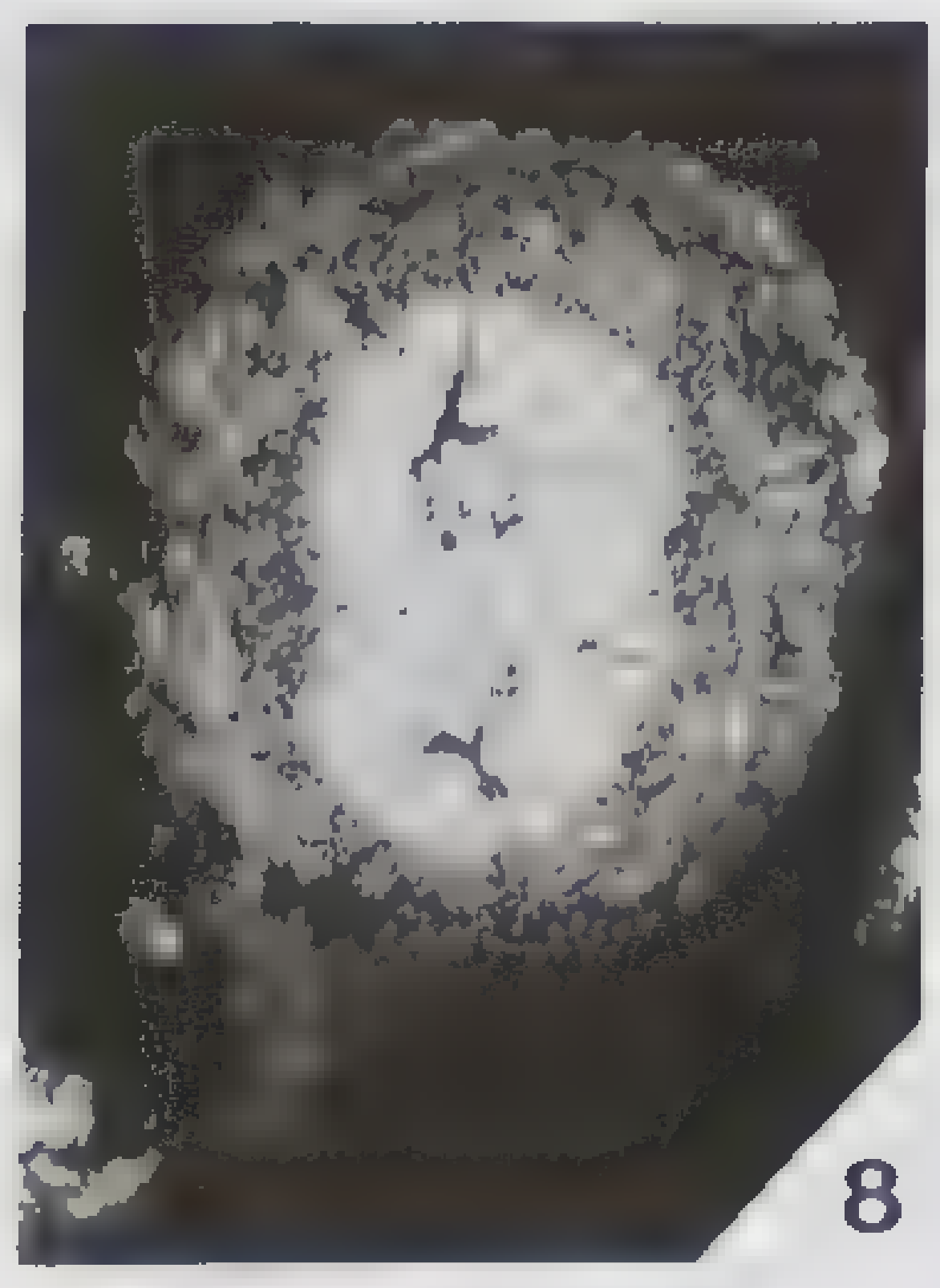
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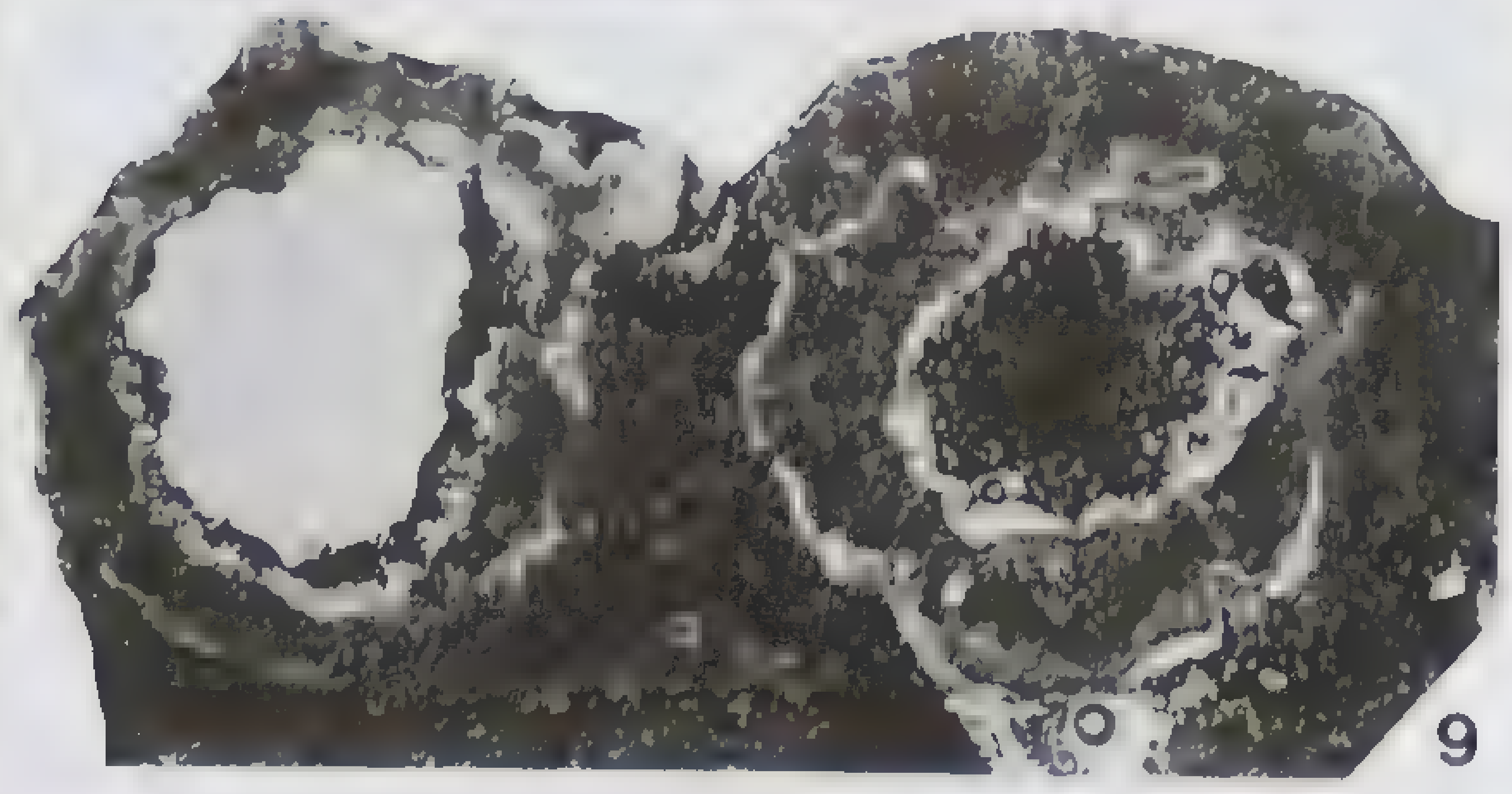
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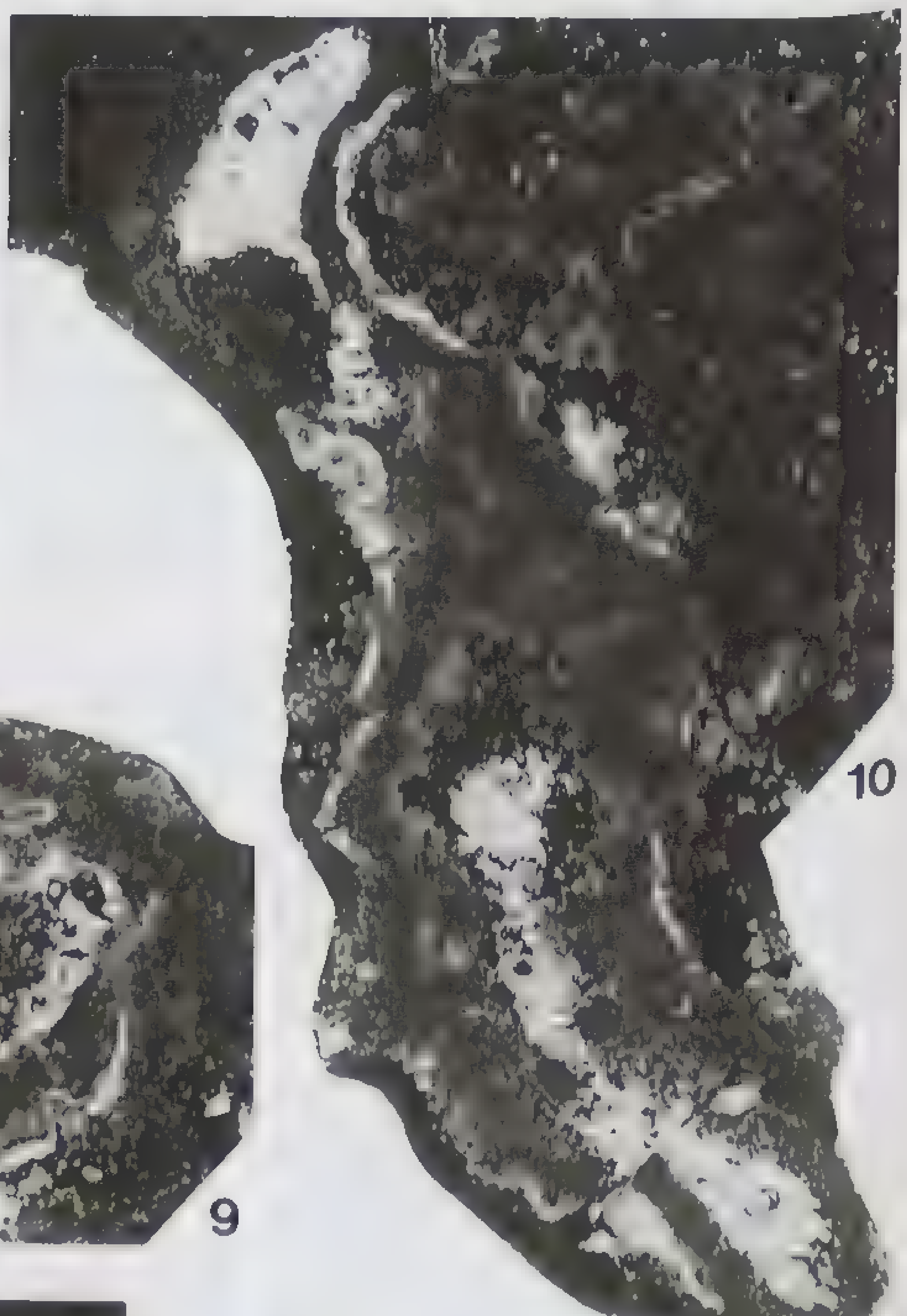
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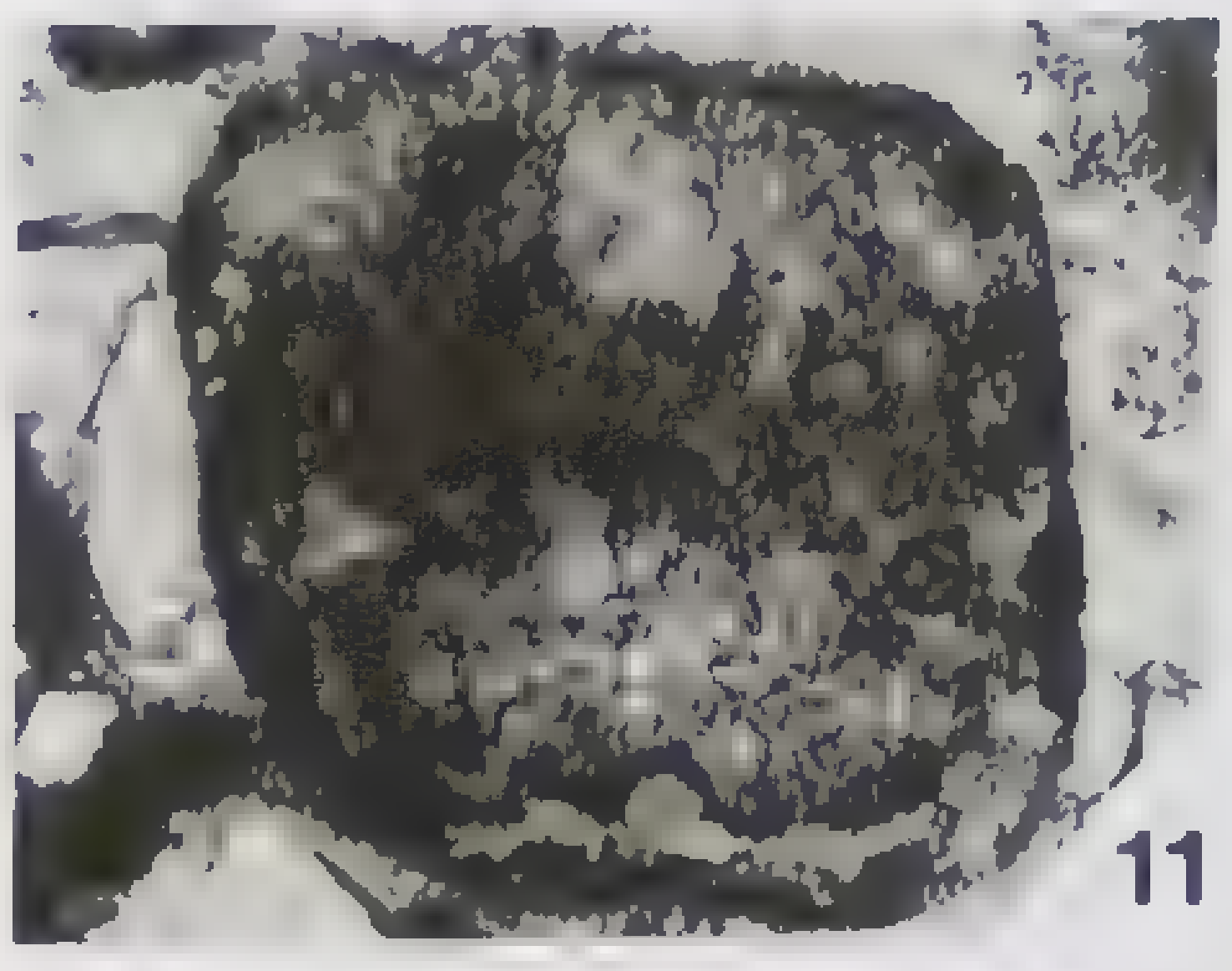
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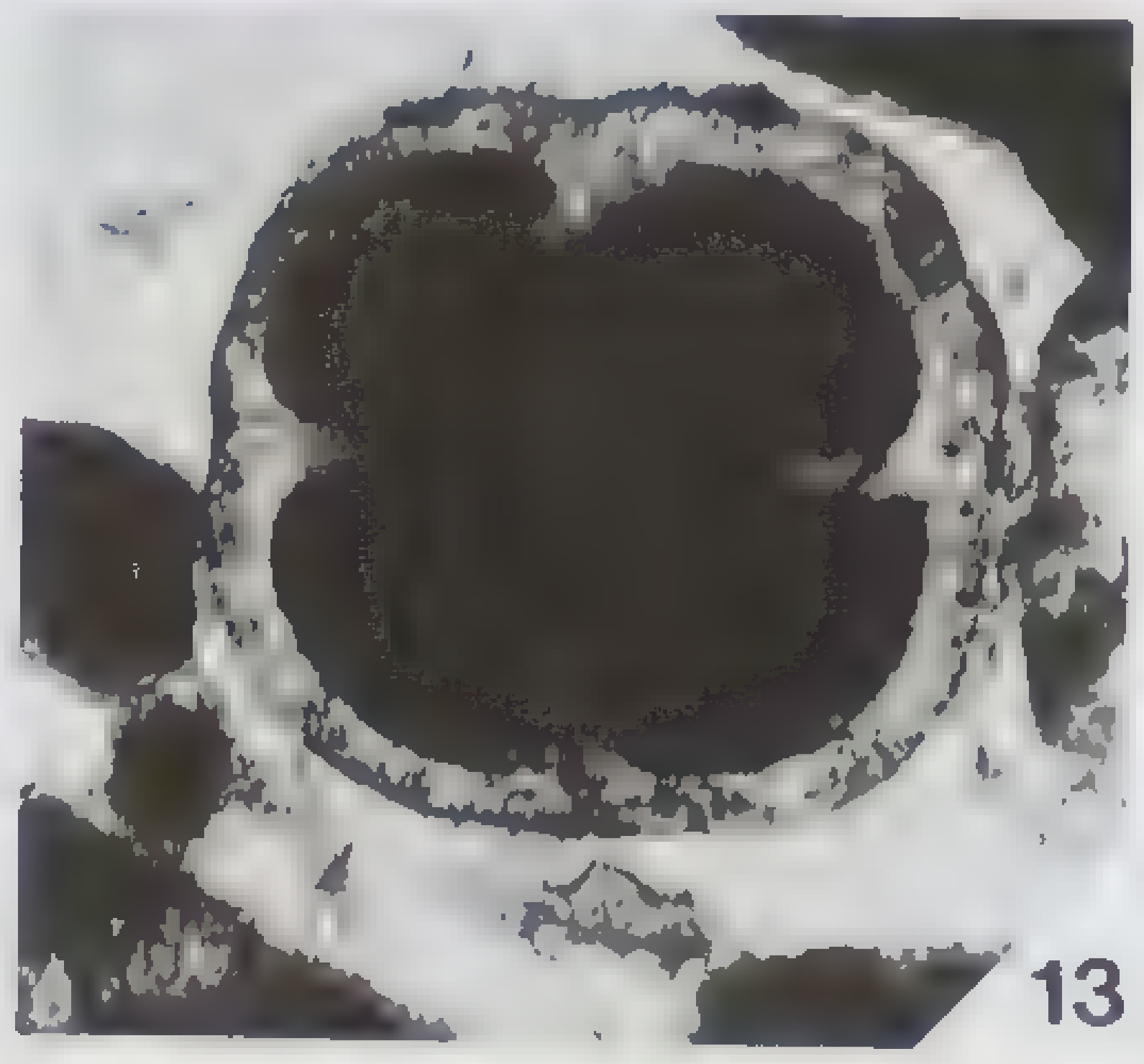
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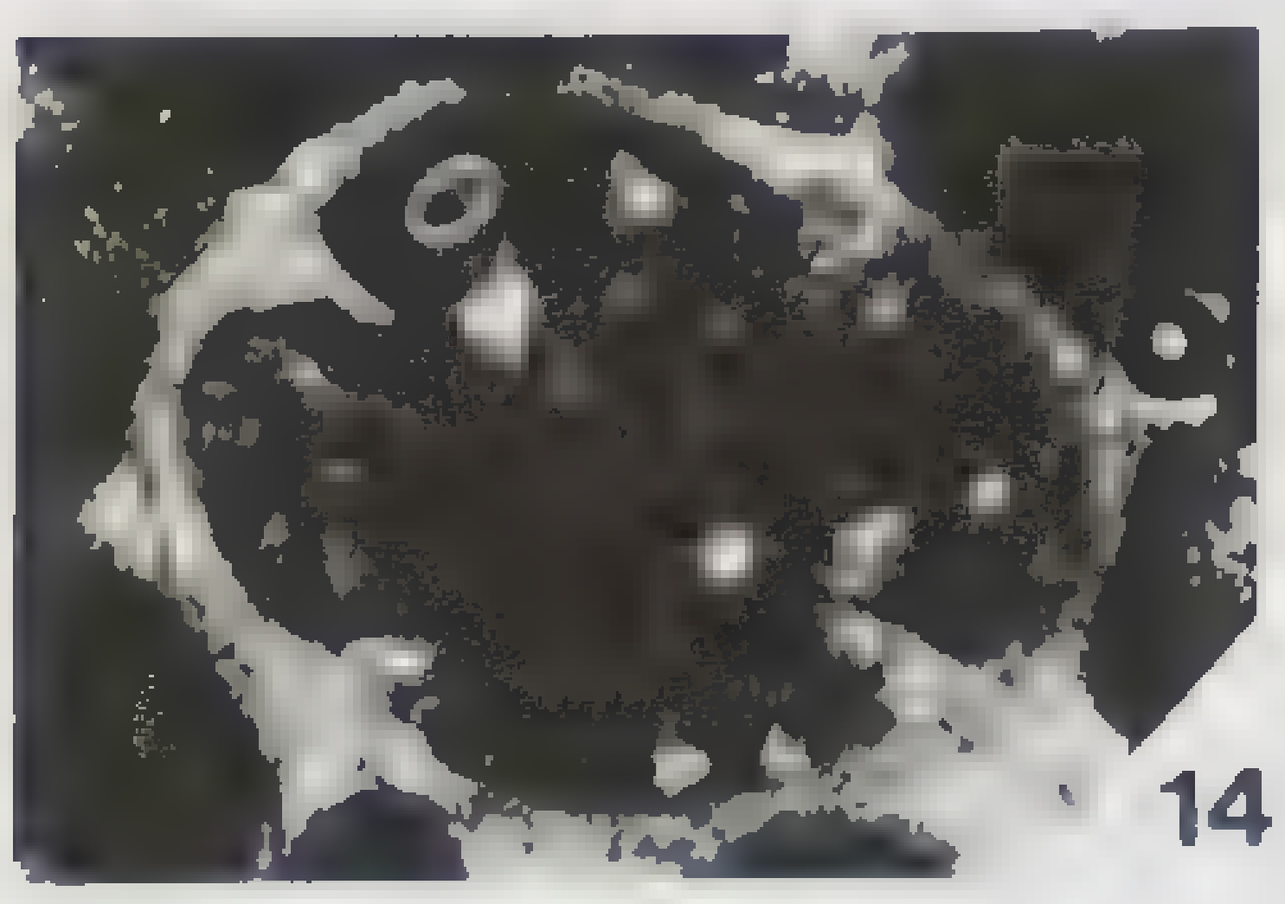
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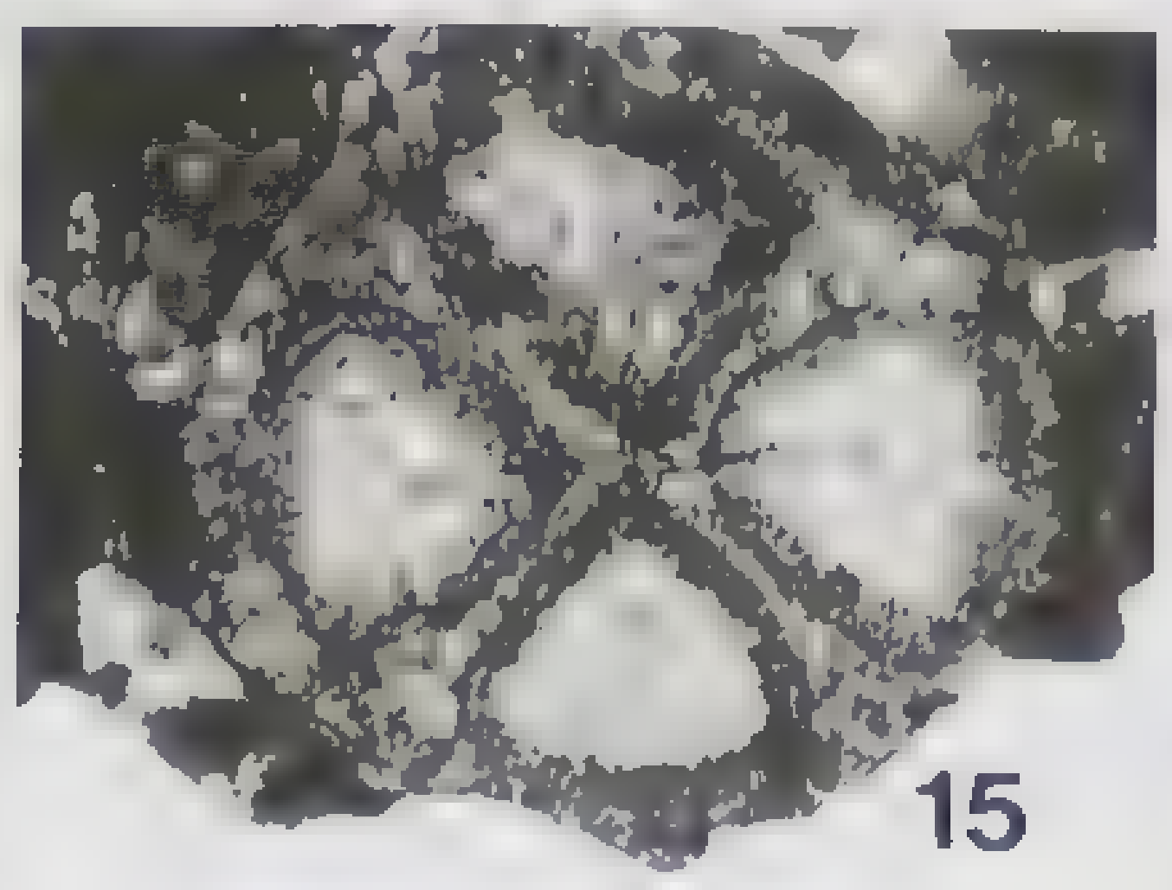
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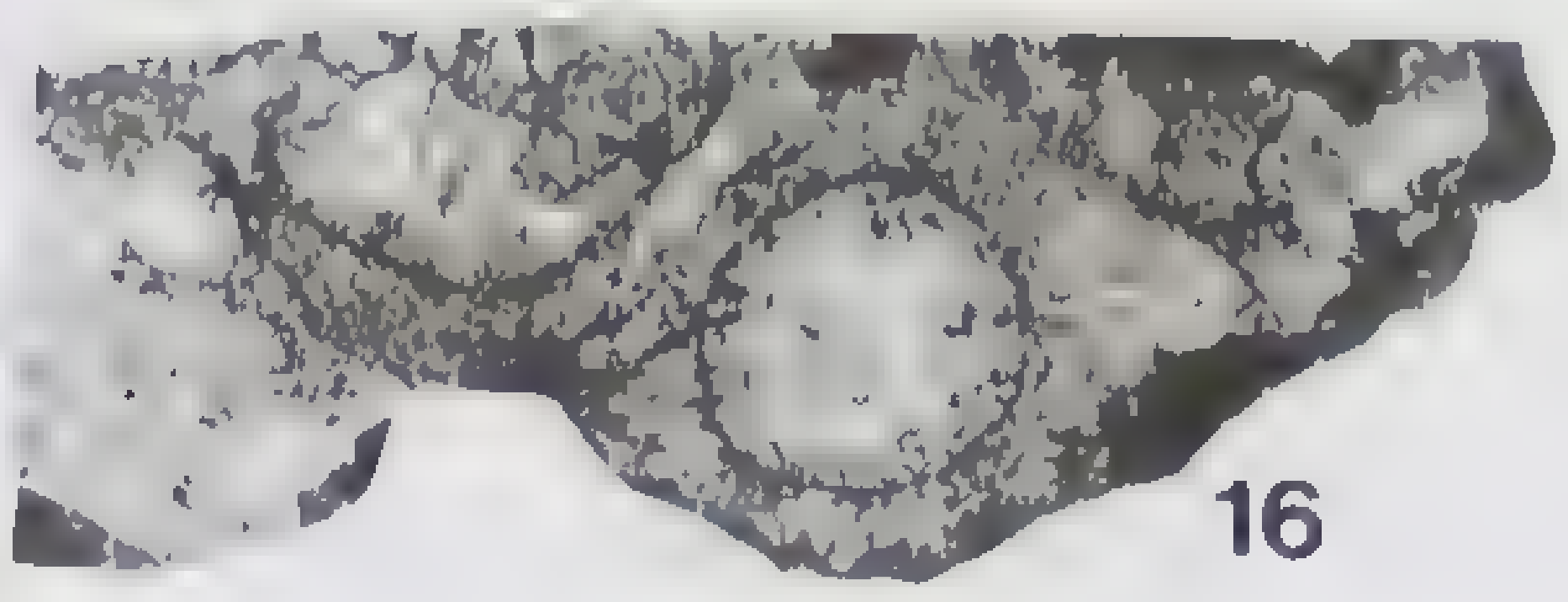
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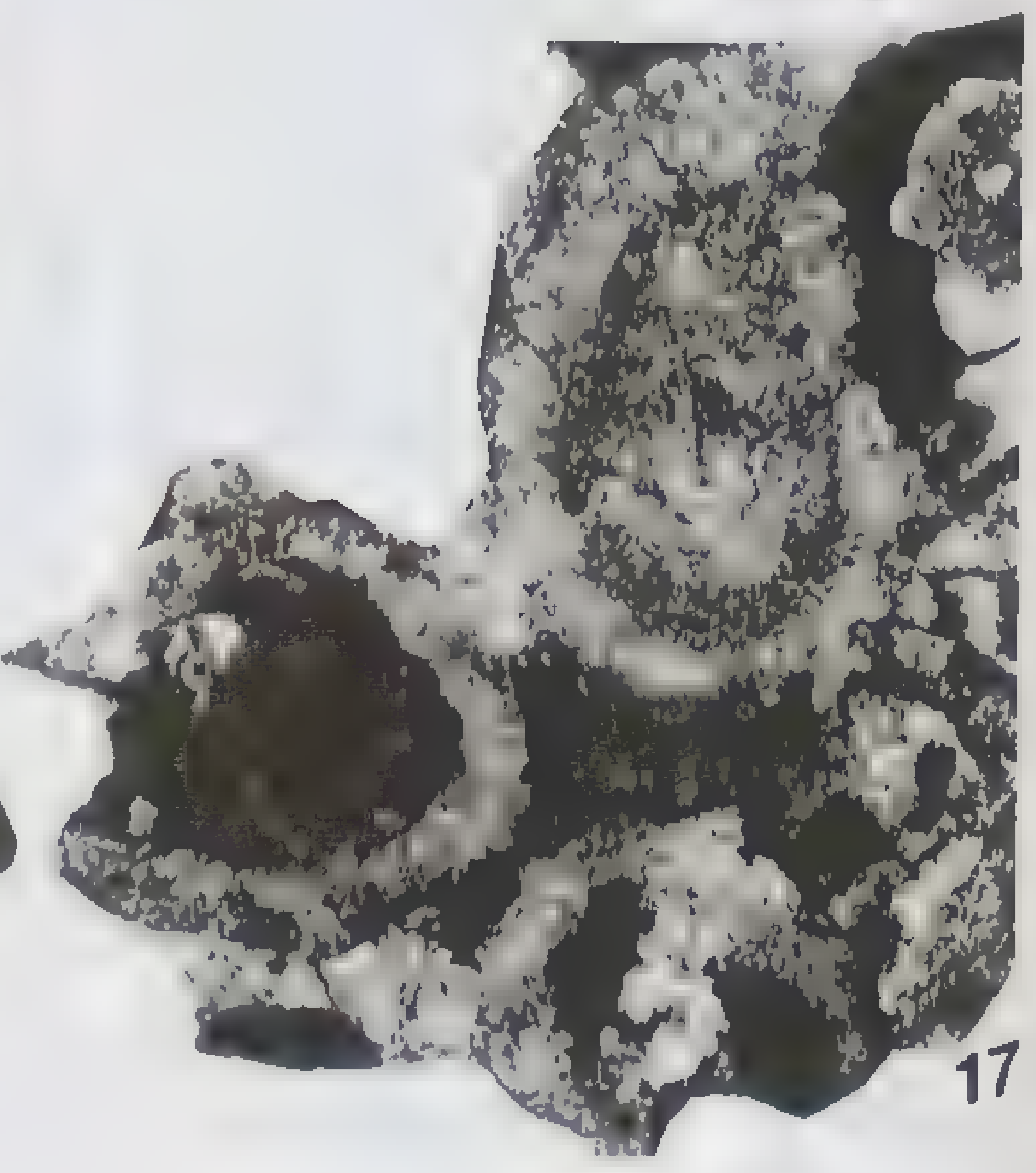
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EXPLANATION OF PLATE 20

Figure Page

1–10. ***Aulopora*** species A 97

[1–8, *Brevilamnulella* beds, Keel Formation, Section-interval 23-2 (Lawrence Quarry) (site 23iv); 9, 10, Wilhelmi Formation, Section-interval 37-1 (Essex).]

1–7. USNM 485785d: 1, transverse, oblique, and longitudinal sections of corallites (note that corallites encrust calcareous algae and one another), ×5; 2, two corallites (seen in longitudinal section) are based upon another corallite (in transverse section), and the corallite on the left has another corallite based upon it (on left), ×8; 3, longitudinal section of a corallite, with another corallite based upon it (on left; detail from above center in 2), ×40; 4, longitudinal section of a corallite, with another corallite based upon it (on left); 5, transverse section, ×15; 6, transverse section showing wall (detail from upper half in 5), ×40; 7, transverse oblique section of two connected corallites (detail from upper right of center in 1, turned 20° clockwise), ×15.

8. USNM 485780d: transverse section, ×40.

9, 10. USNM 485952: 9, transverse section, ×15; 10, longitudinal section of two connected corallites, ×15.

11–17. ***Rhabdotetradium*** species A 99

[11–13, Leemon Formation, Section-interval 20-3 (Short Farm); 14–17, Leemon Formation, Section-interval 31-1 (Thebes North).]

11–13. USNM 423401: serial transverse sections from a single corallite, in order from lowest to highest, ×40.

14. USNM 485770b: transverse section, ×40.

15–17. USNM 485953: serial transverse sections showing increase, ×40.

EXPLANATION OF PLATE 21

Figure		Page
1–14.	**Palaeophyllum** species	101

[1–3, oölite of Keel Formation, Section-interval 23-3 (Lawrence Quarry) (site 23i); 4, Kissenger Limestone Member, Bryant Knob Formation, Section-interval 15-1 (Calumet); 5, 10–14, Kissenger Limestone Member, Bryant Knob Formation, Section-interval 14-2 (Higginbotham Farm); 6–9, Kissenger Limestone Member, Bryant Knob Formation, Section-interval 14-1 (Higginbotham Farm).]

1–3. USNM 485954: serial transverse sections through a group of corallites, in order from lowest to highest, × 7.

4. USNM 485955: transverse section, × 7.

5. USNM 485959: transverse section, × 7.

6–9. USNM 485956: 6, 7, transverse sections, × 7; 8, transverse section showing structure of wall and septa (detail from upper half in 6, turned 20° clockwise), × 40; 9, longitudinal section, × 7; all from a single corallite.

10–12. USNM 485957: 10, 11, transverse sections, × 7; 12, longitudinal section, × 7; all from a single corallite (note epizoic bryozoan).

13, 14. USNM 485958: 13, transverse section, × 7; 14, longitudinal section, × 7; both from a single corallite.

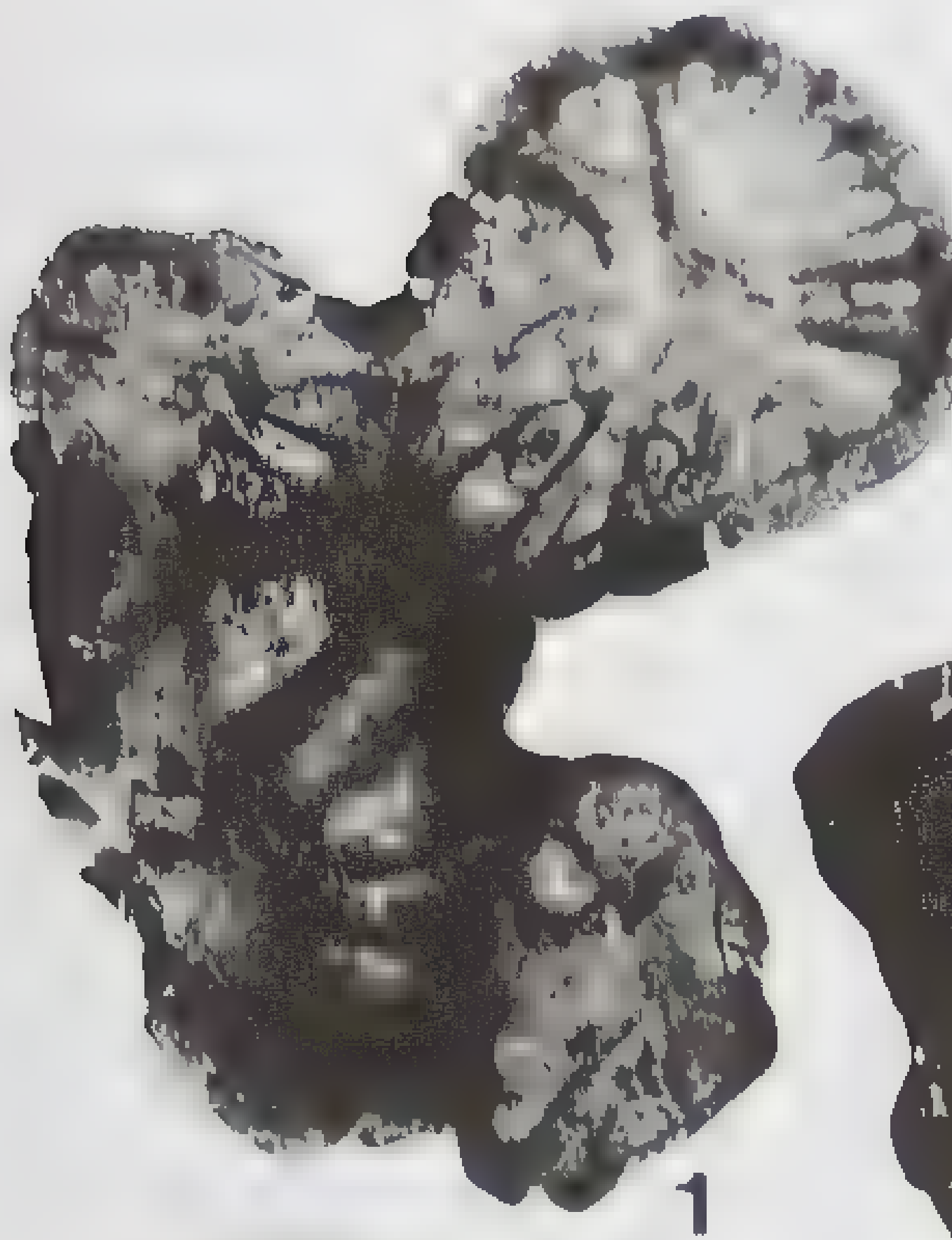
15–25. **Pycnostylus** species A 102

[15–25, channel-fill beds of Mosalem Formation, Section-interval 32-1b (Thomson East).]

15–17. USNM 485960: 15, transverse section, × 15; 16, transverse section, × 4; 17, transverse section (detail from upper right side in 16, turned 20° clockwise), × 20.

18–22. USNM 485966: 18, exterior view of broken longitudinal surface, × 2; 19, longitudinal and oblique section, × 7; 20, transverse section showing connected corallites, × 15; 21, transverse section, × 7; 22, transverse section, × 7.

23–25. USNM 485961: 23, transverse section, × 7; 24, longitudinal section, × 7; 25, transverse section (detail from left side in 23), × 15.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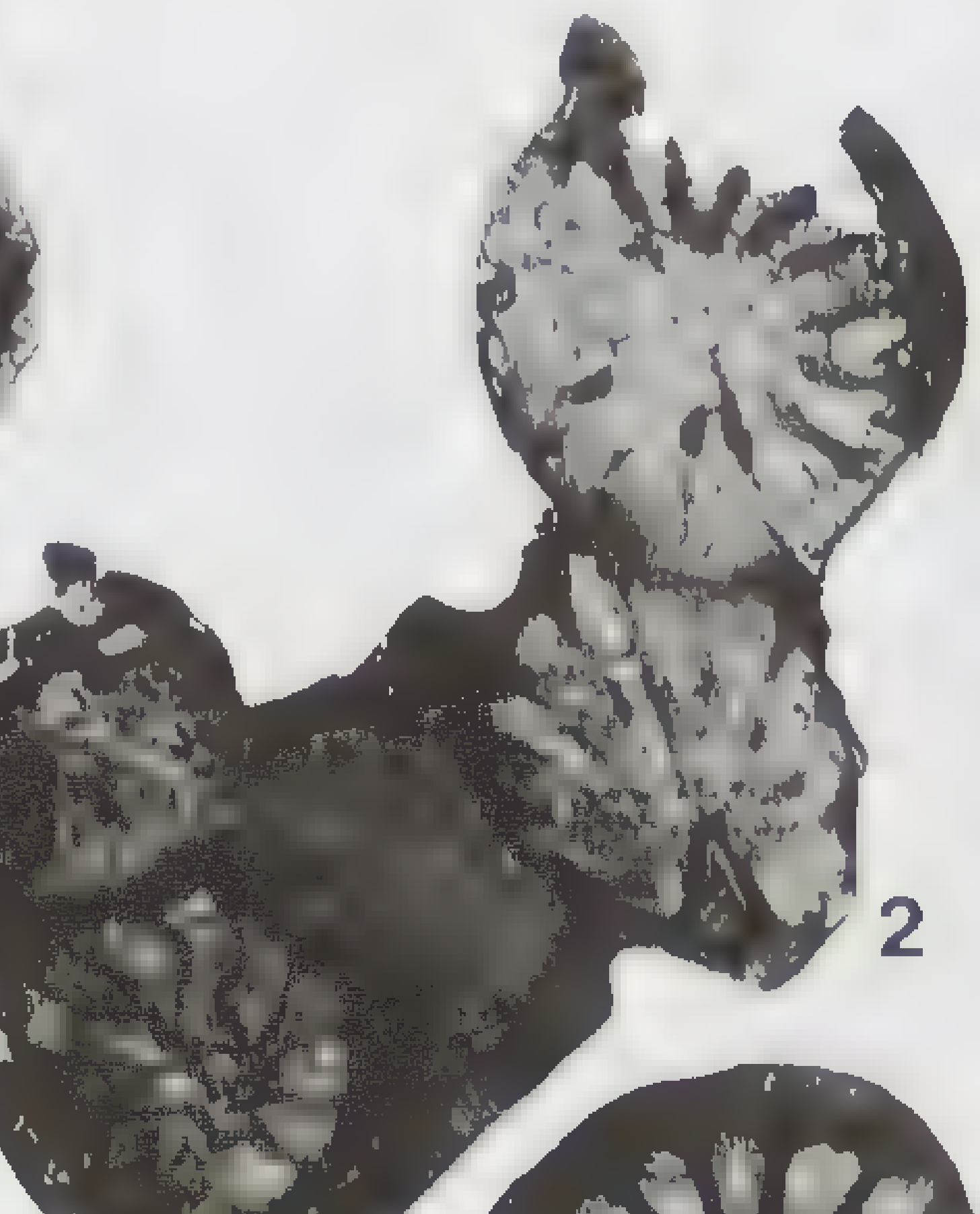
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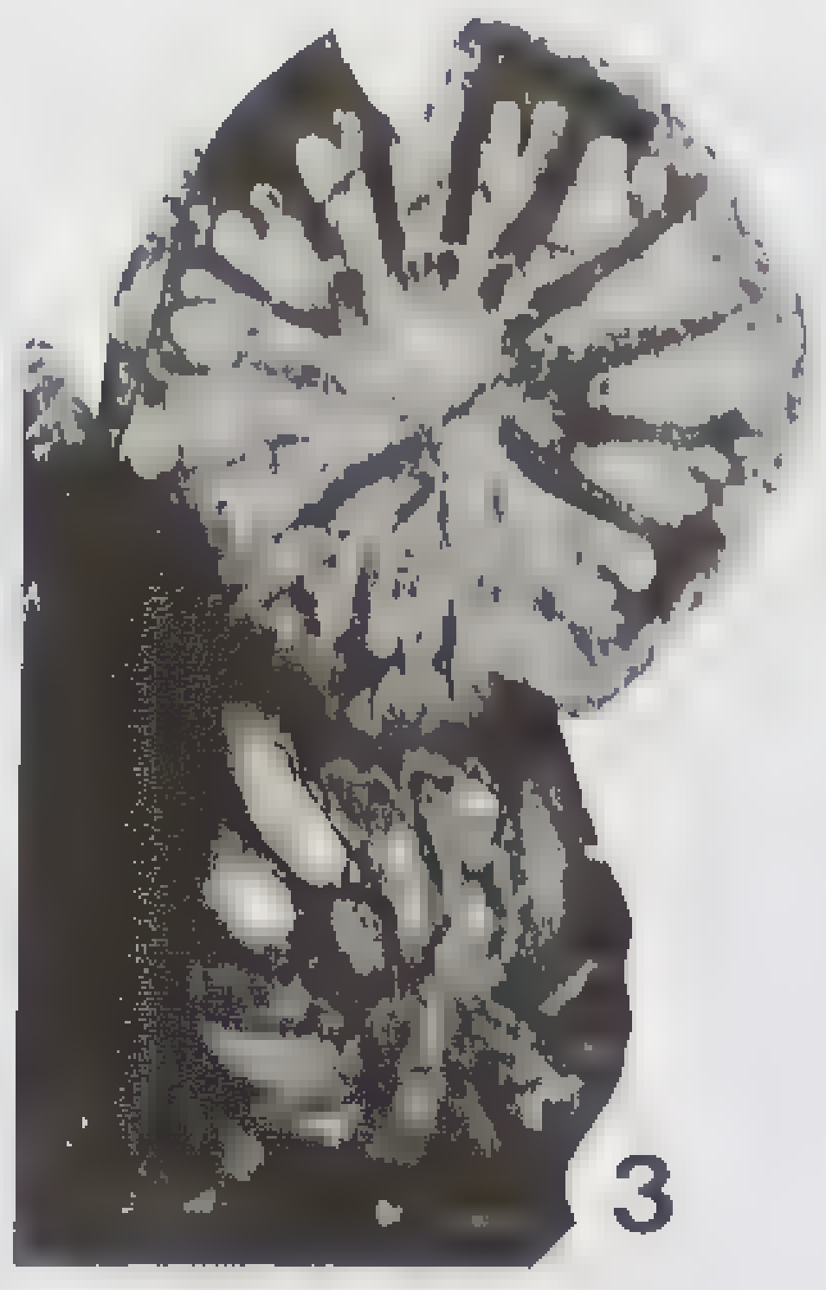
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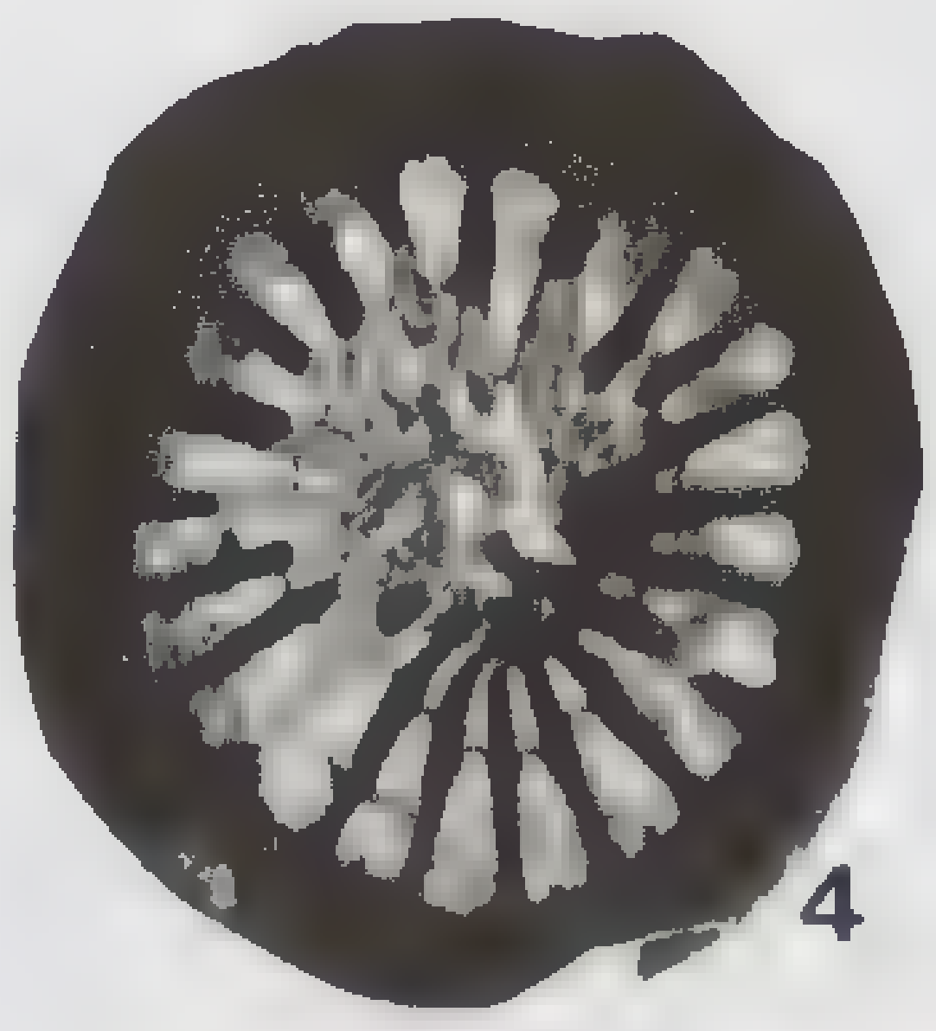
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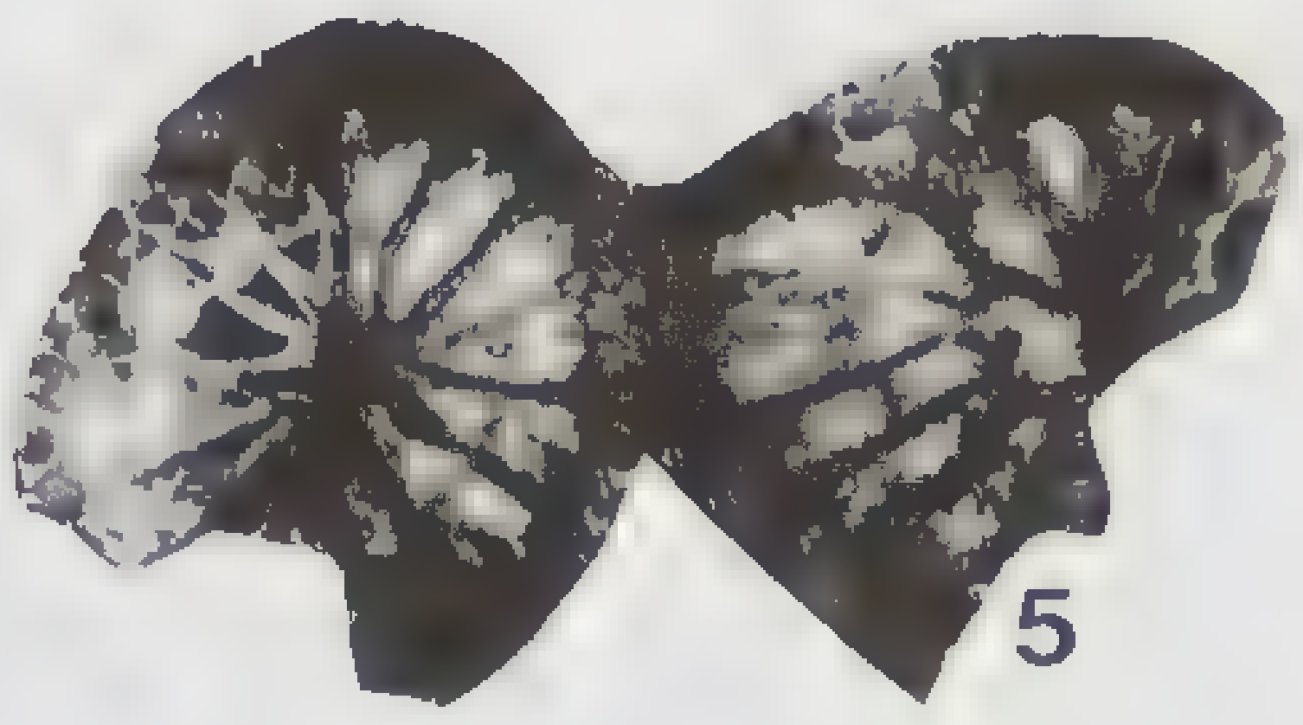
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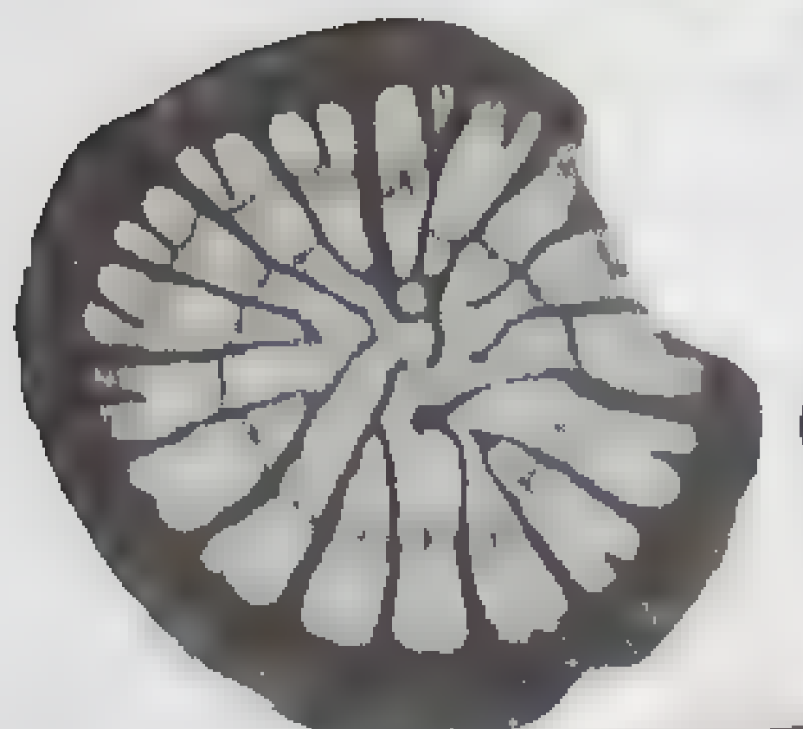
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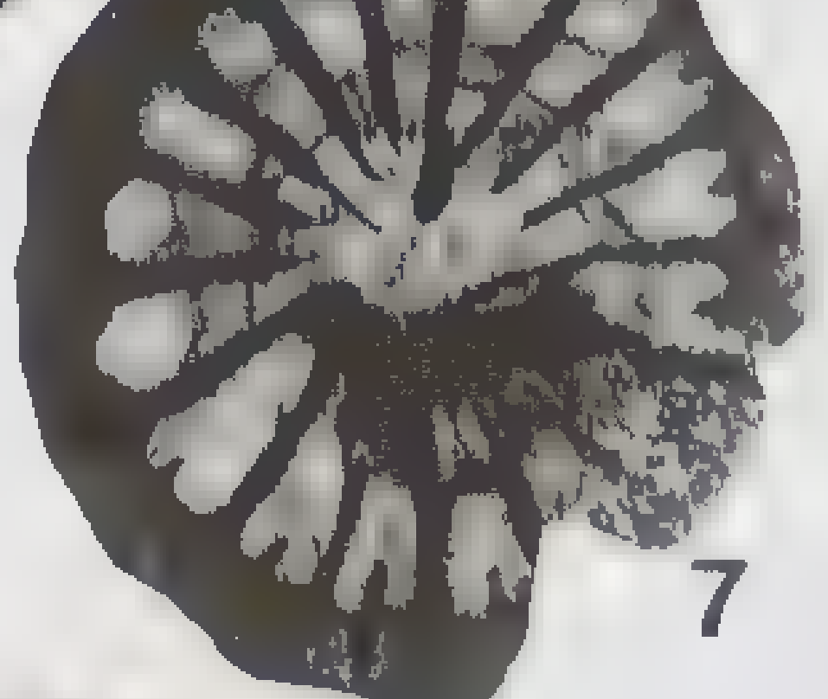
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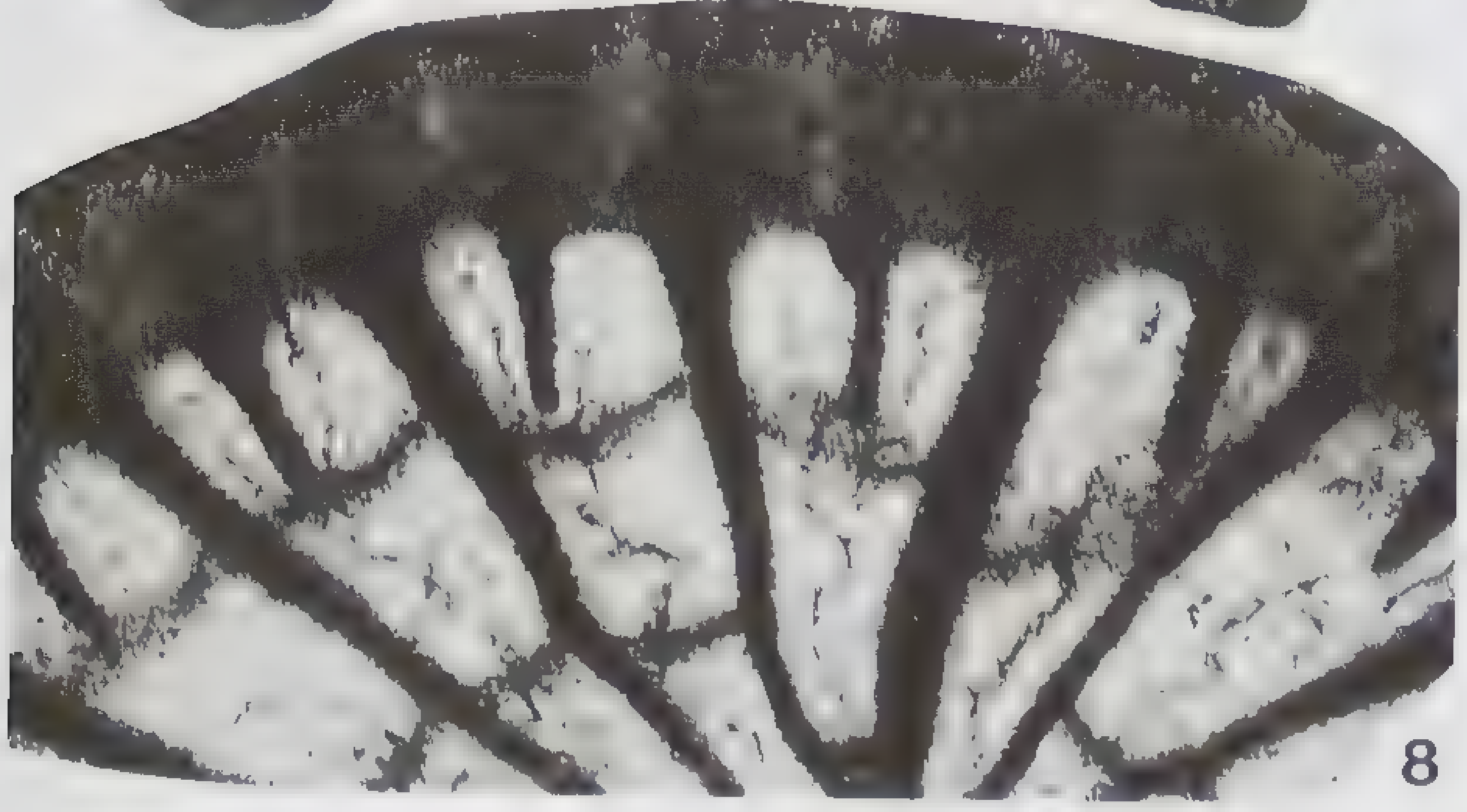
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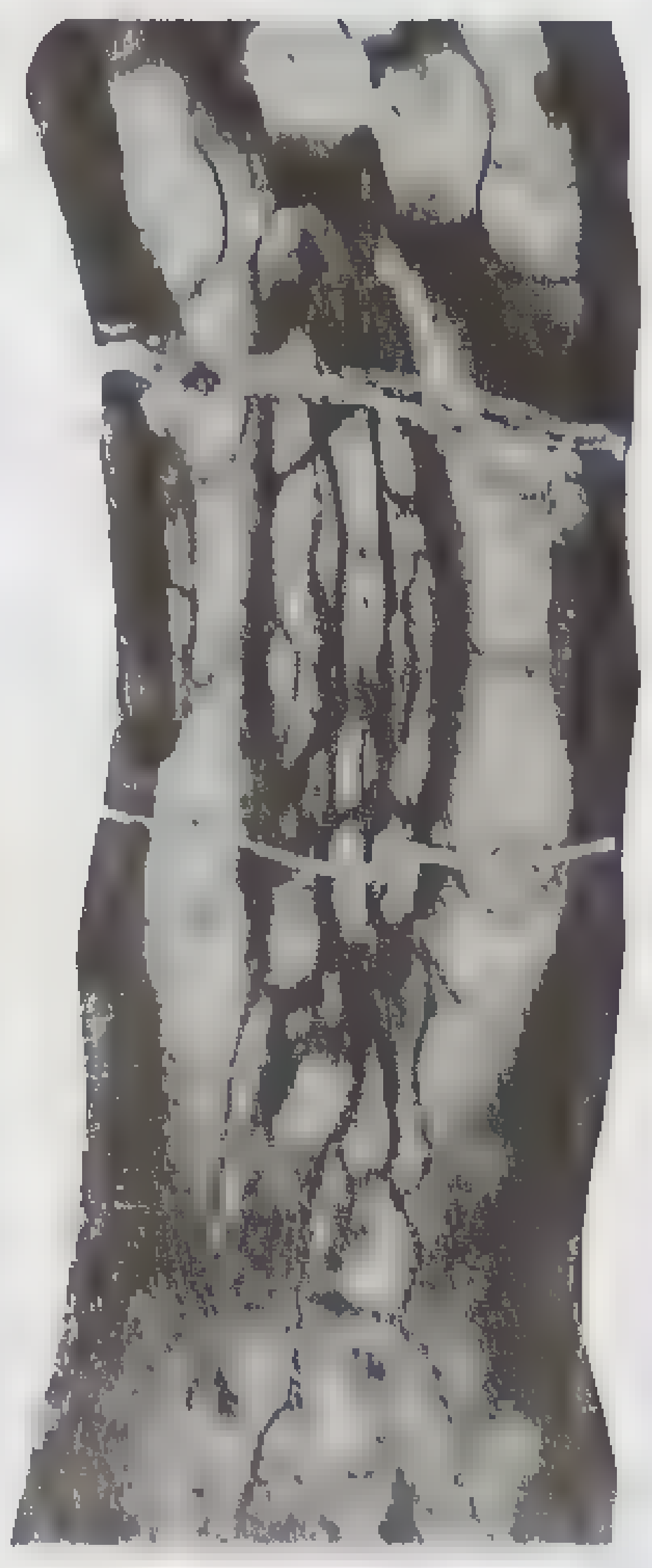
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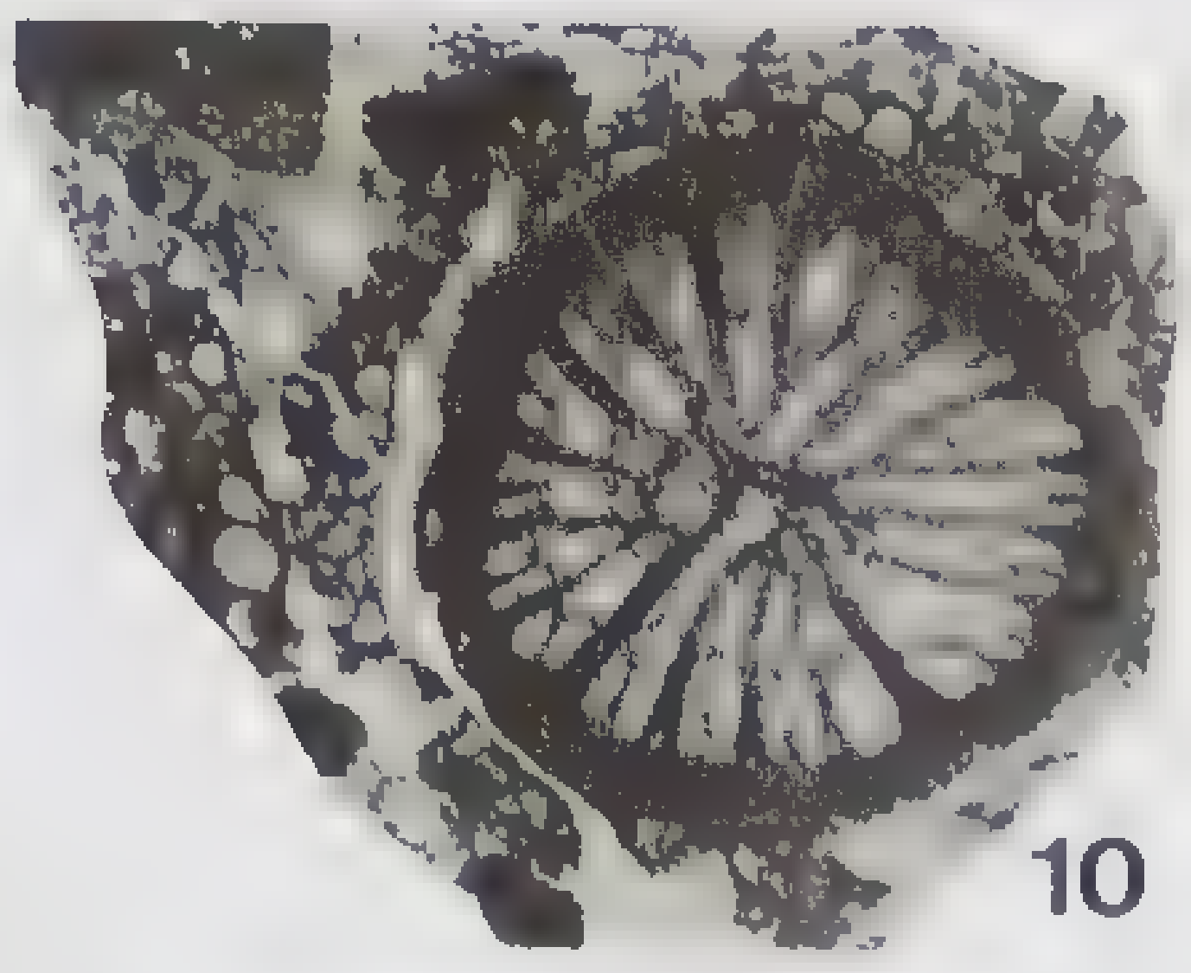
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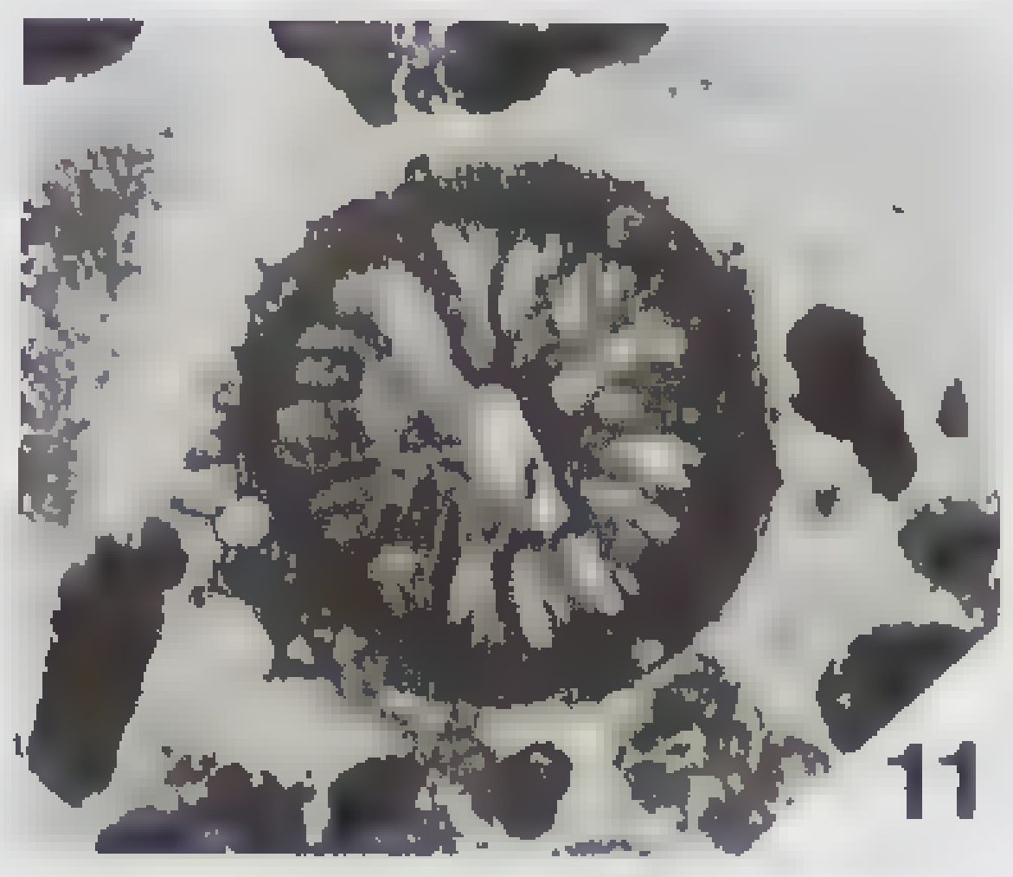
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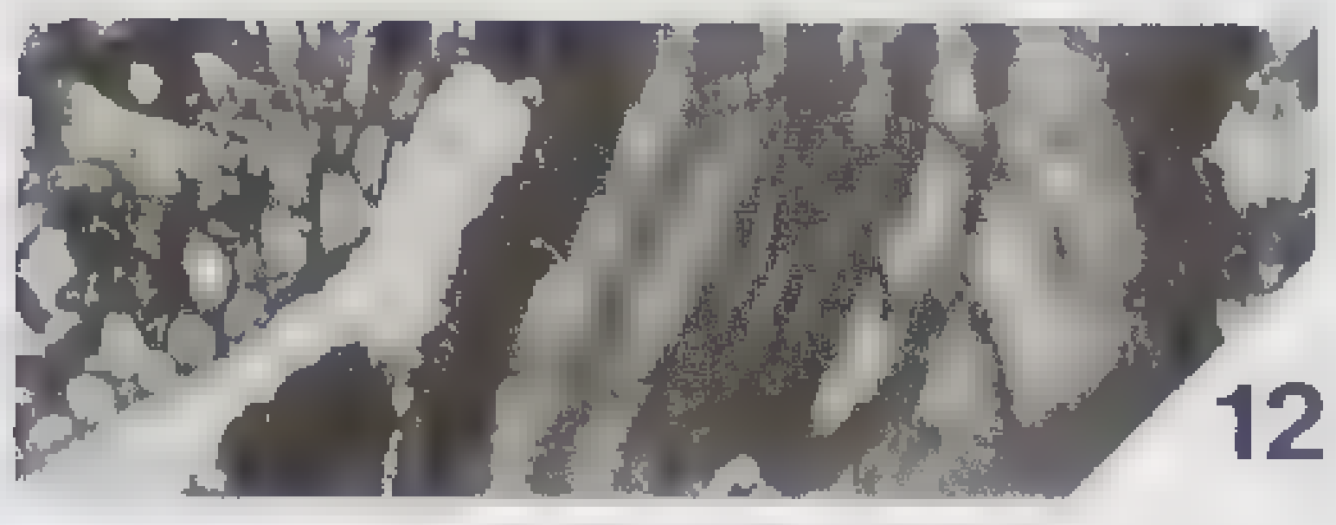
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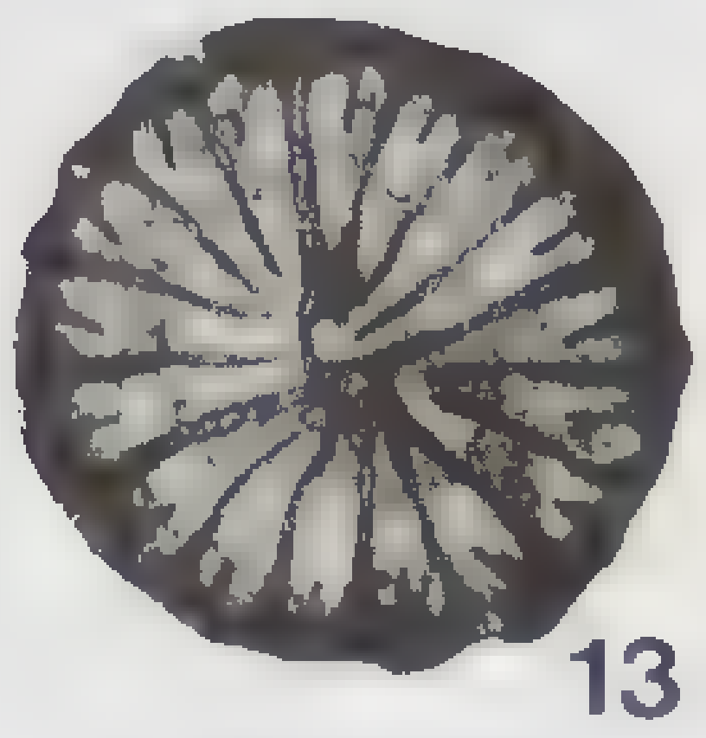
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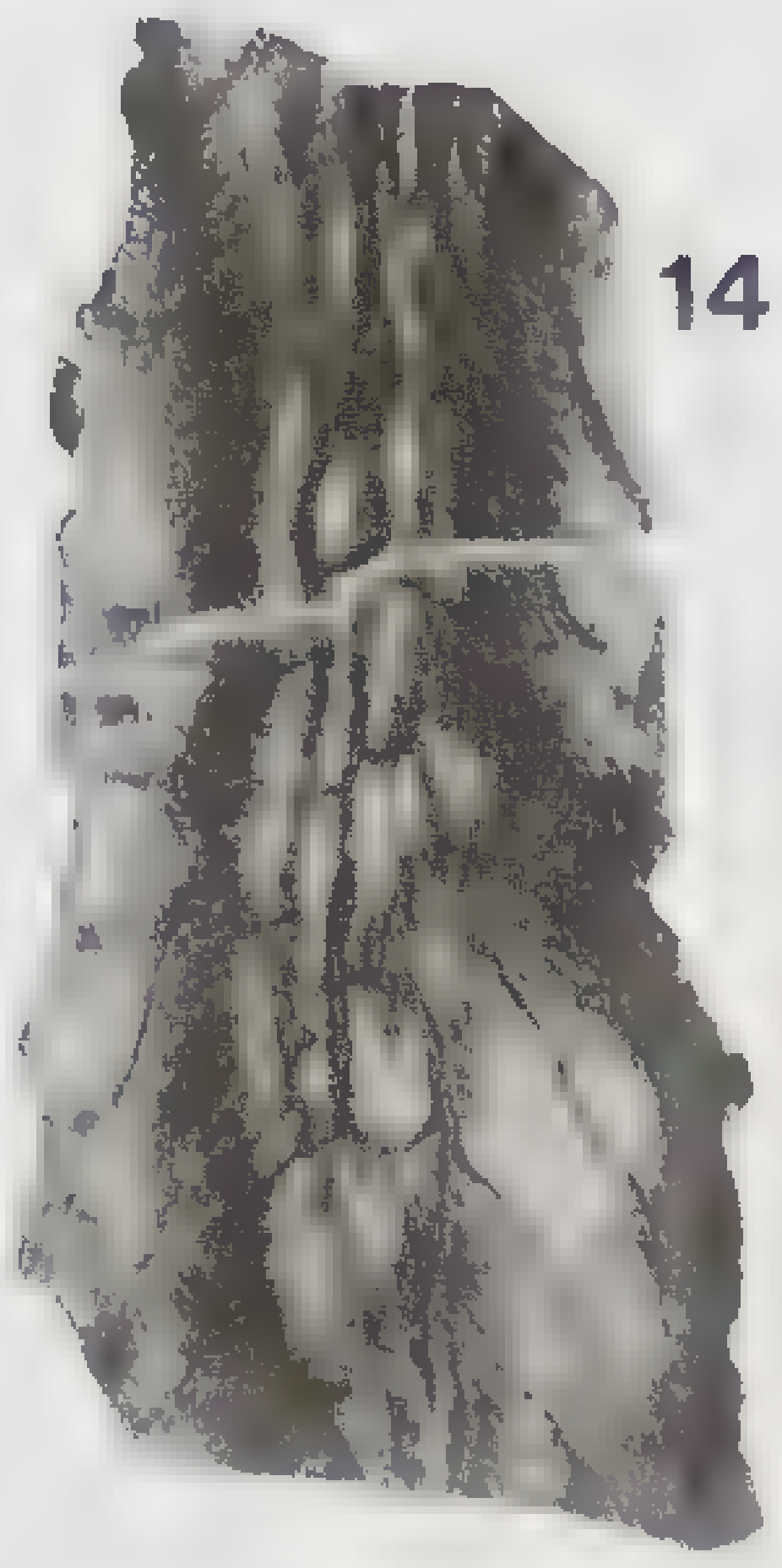
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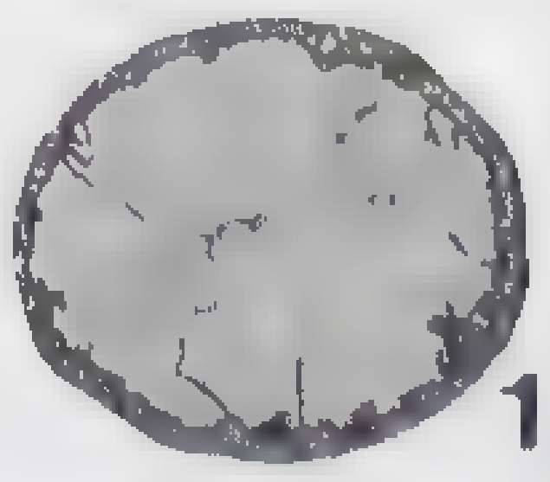
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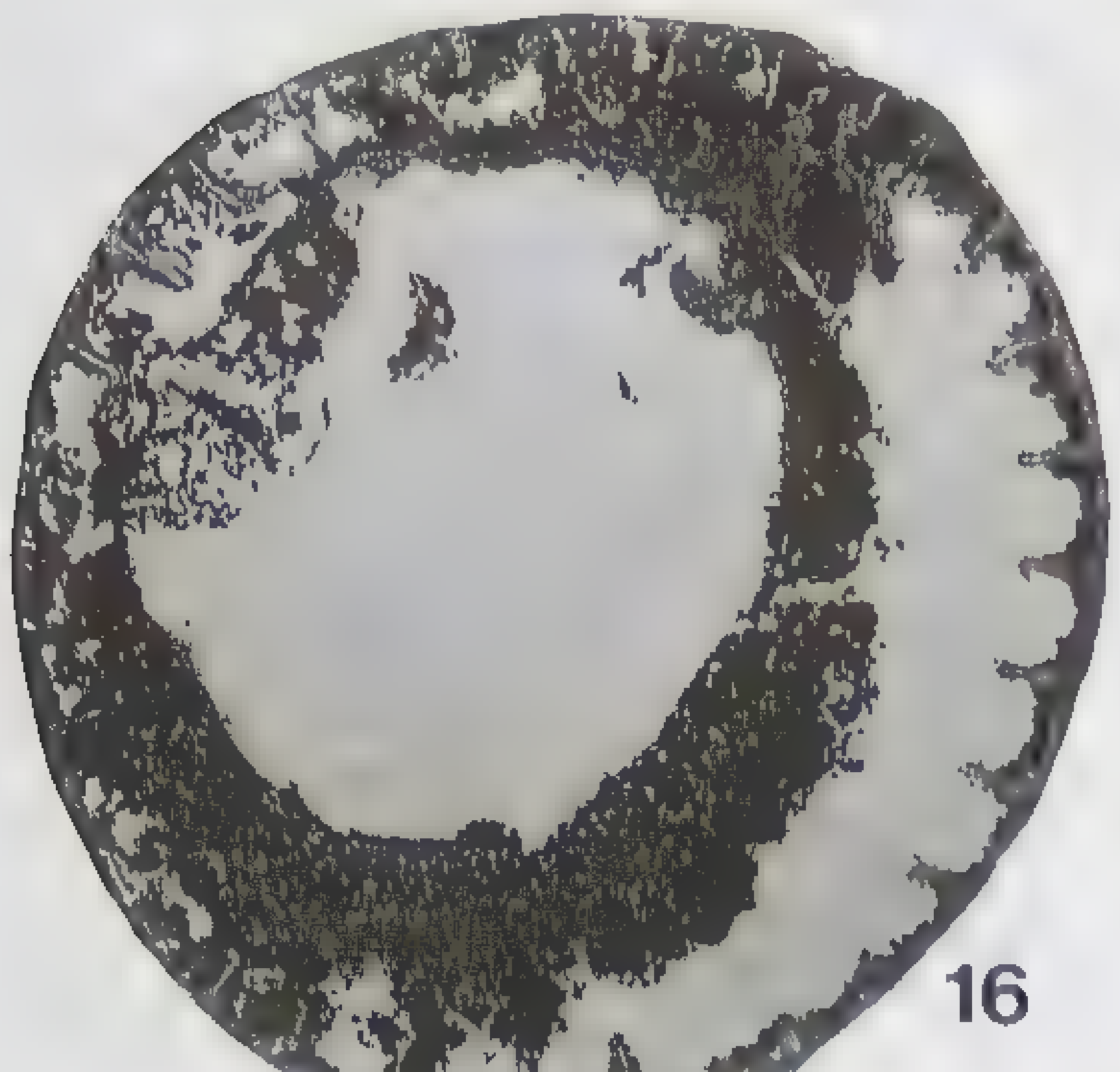
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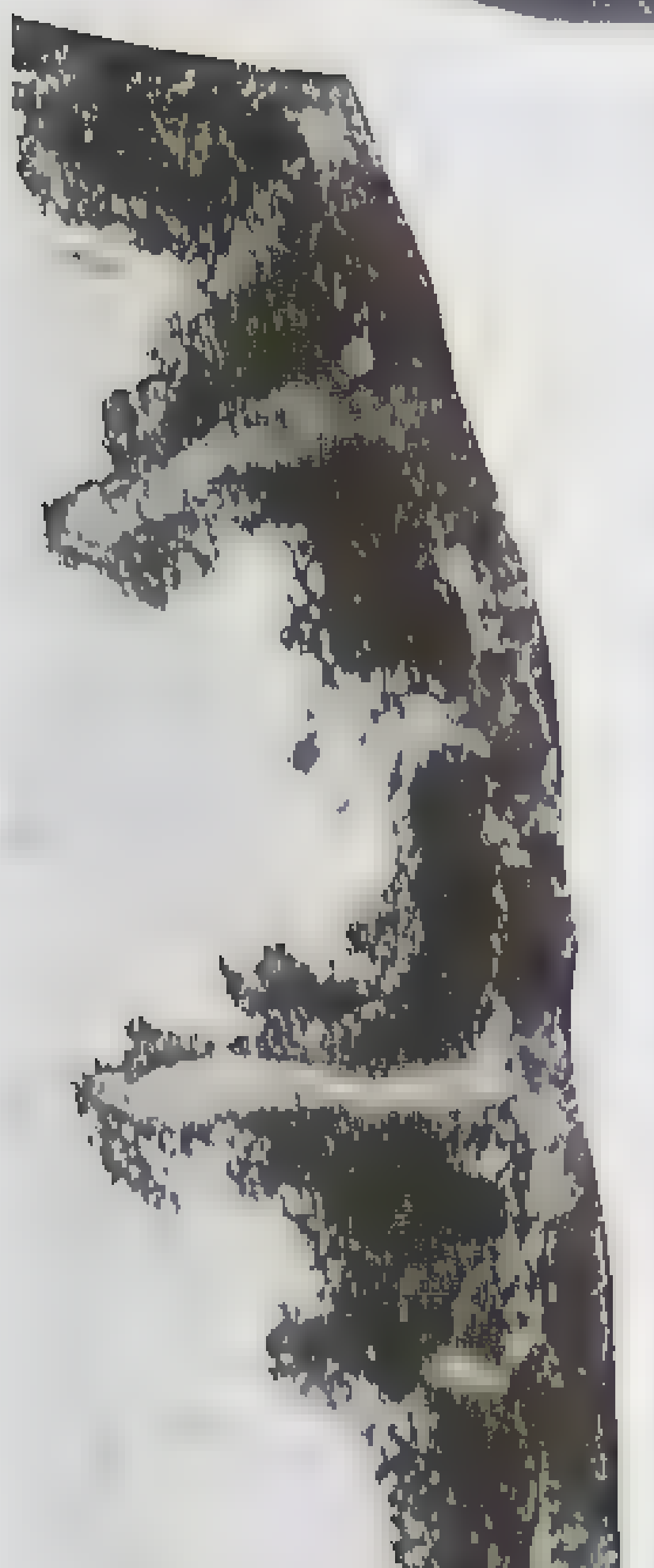
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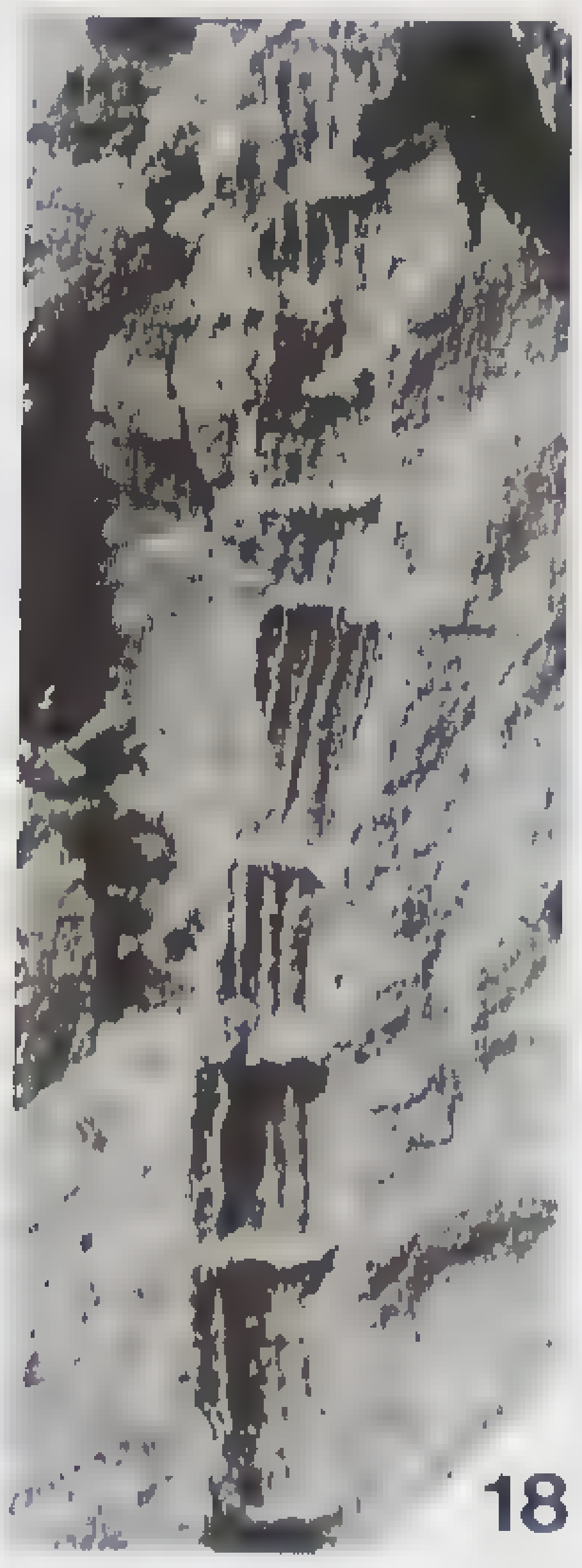
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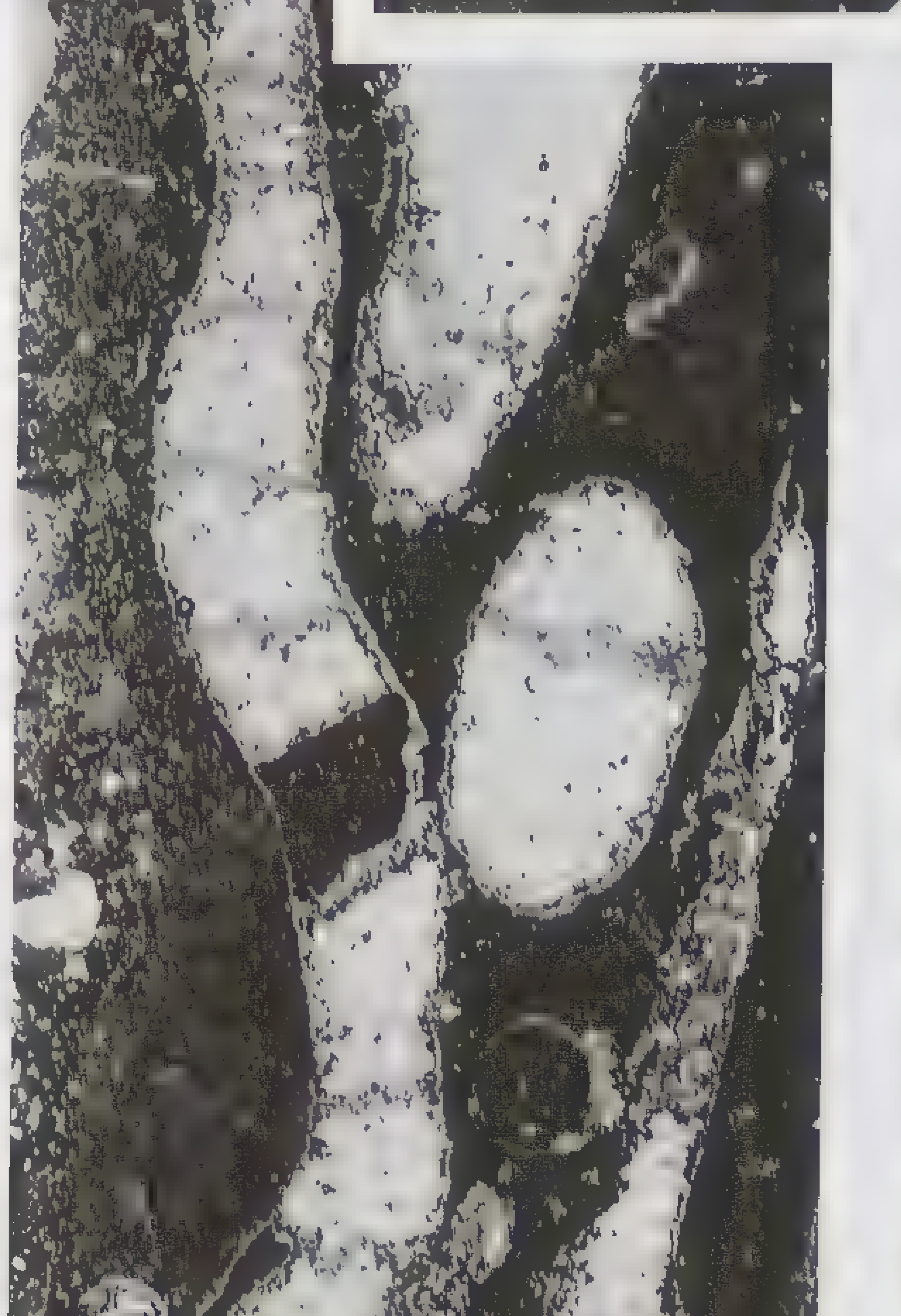
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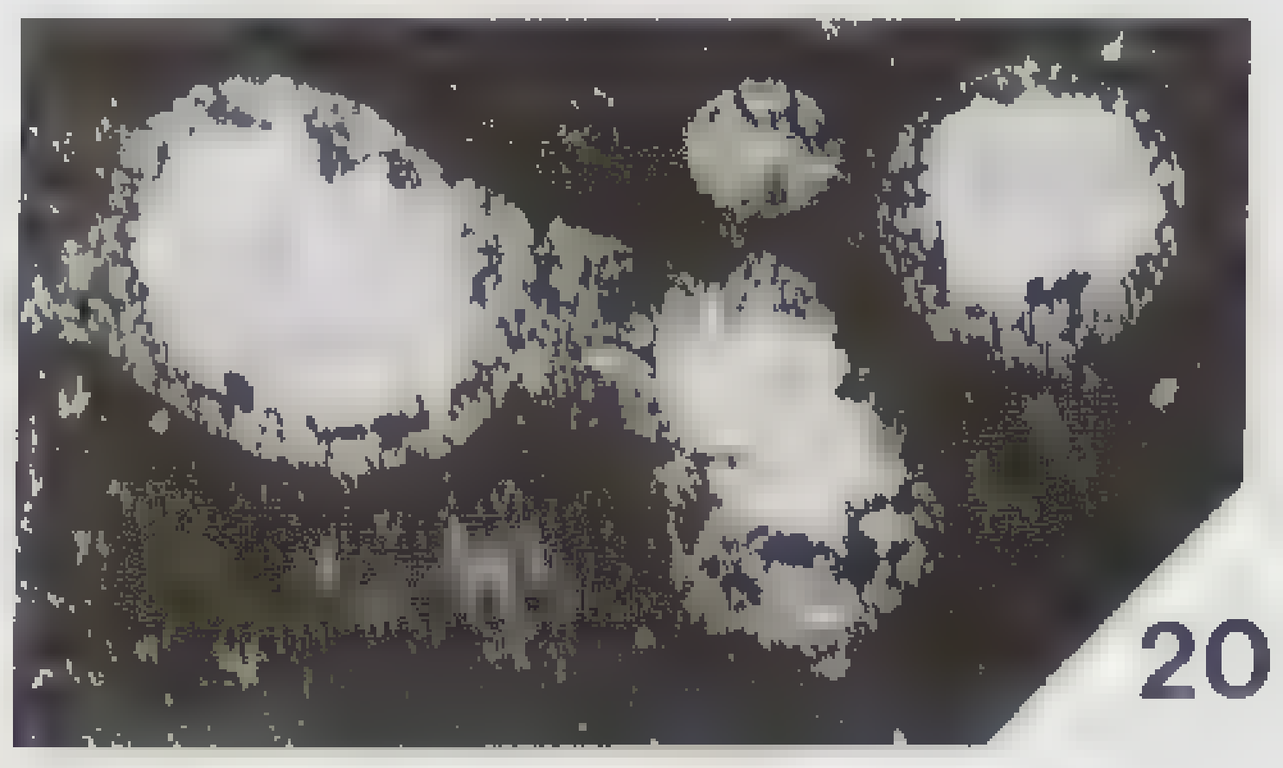
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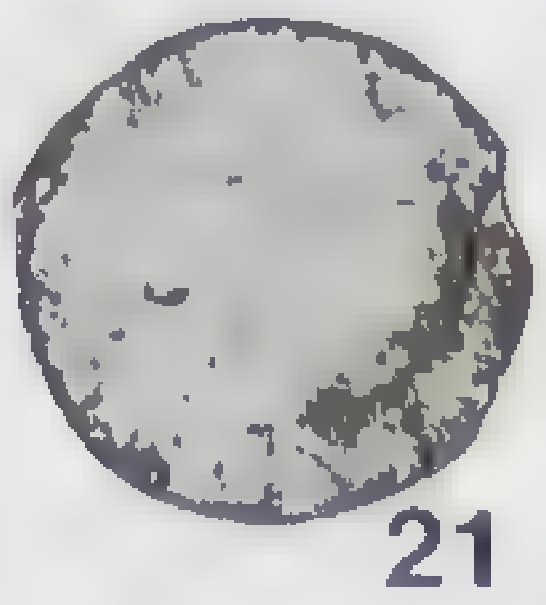
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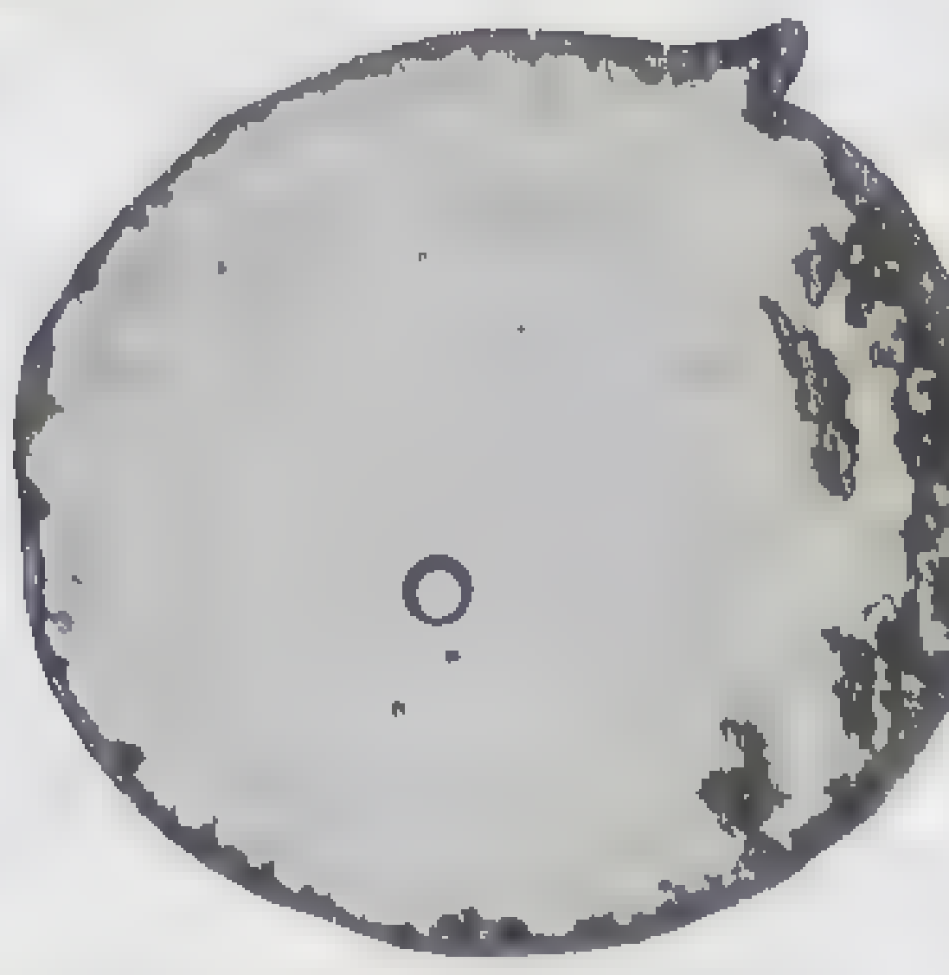
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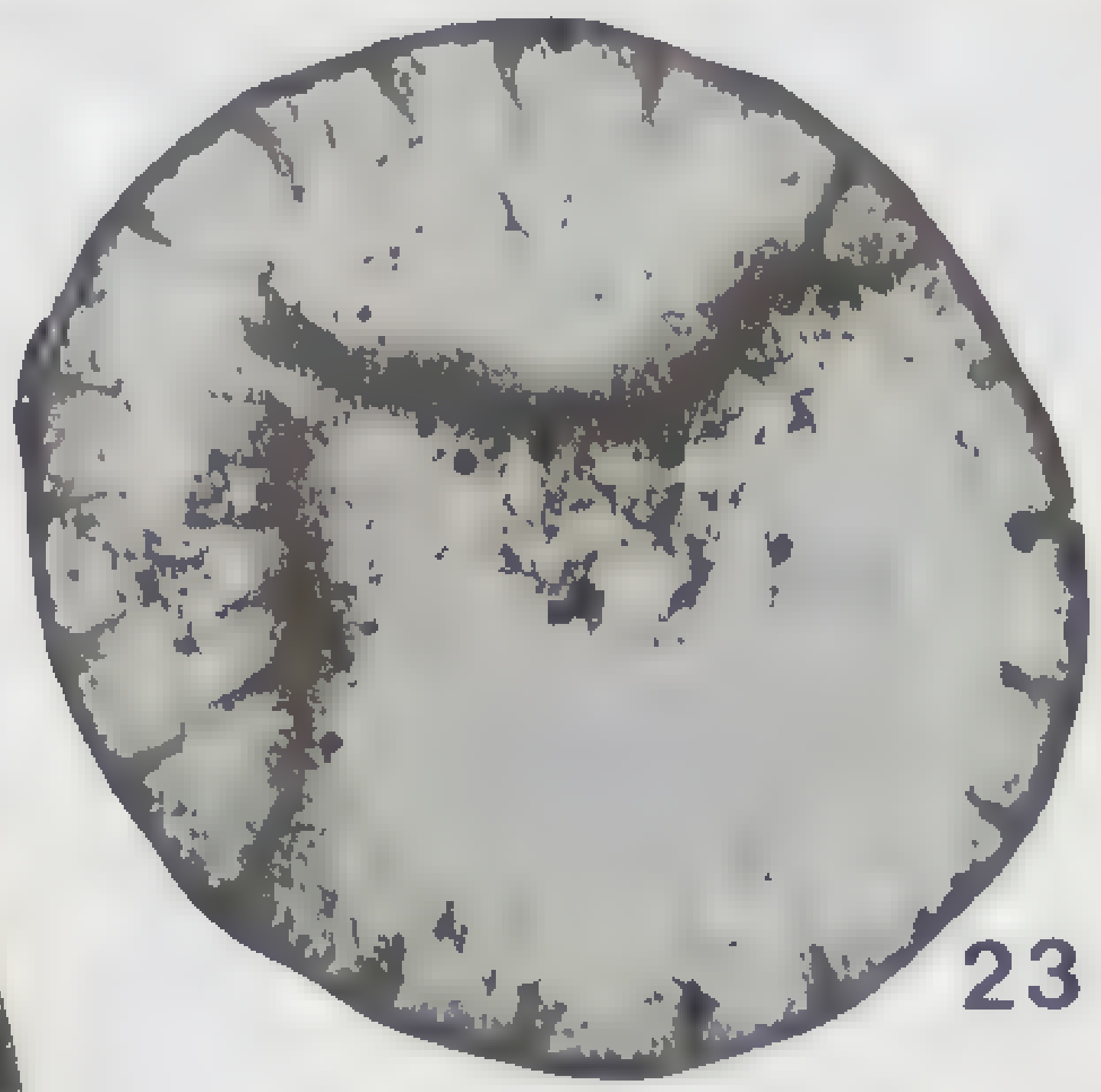
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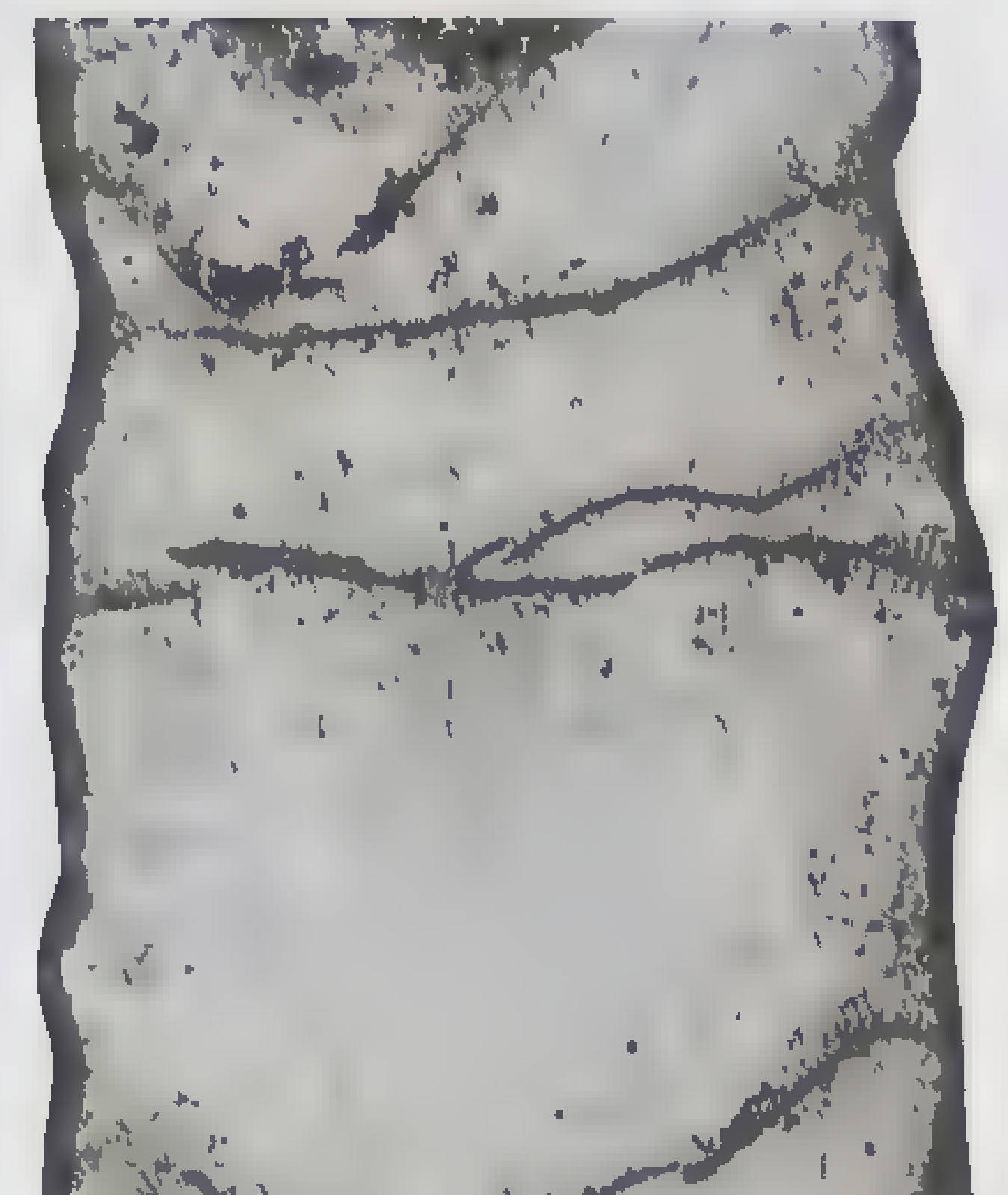
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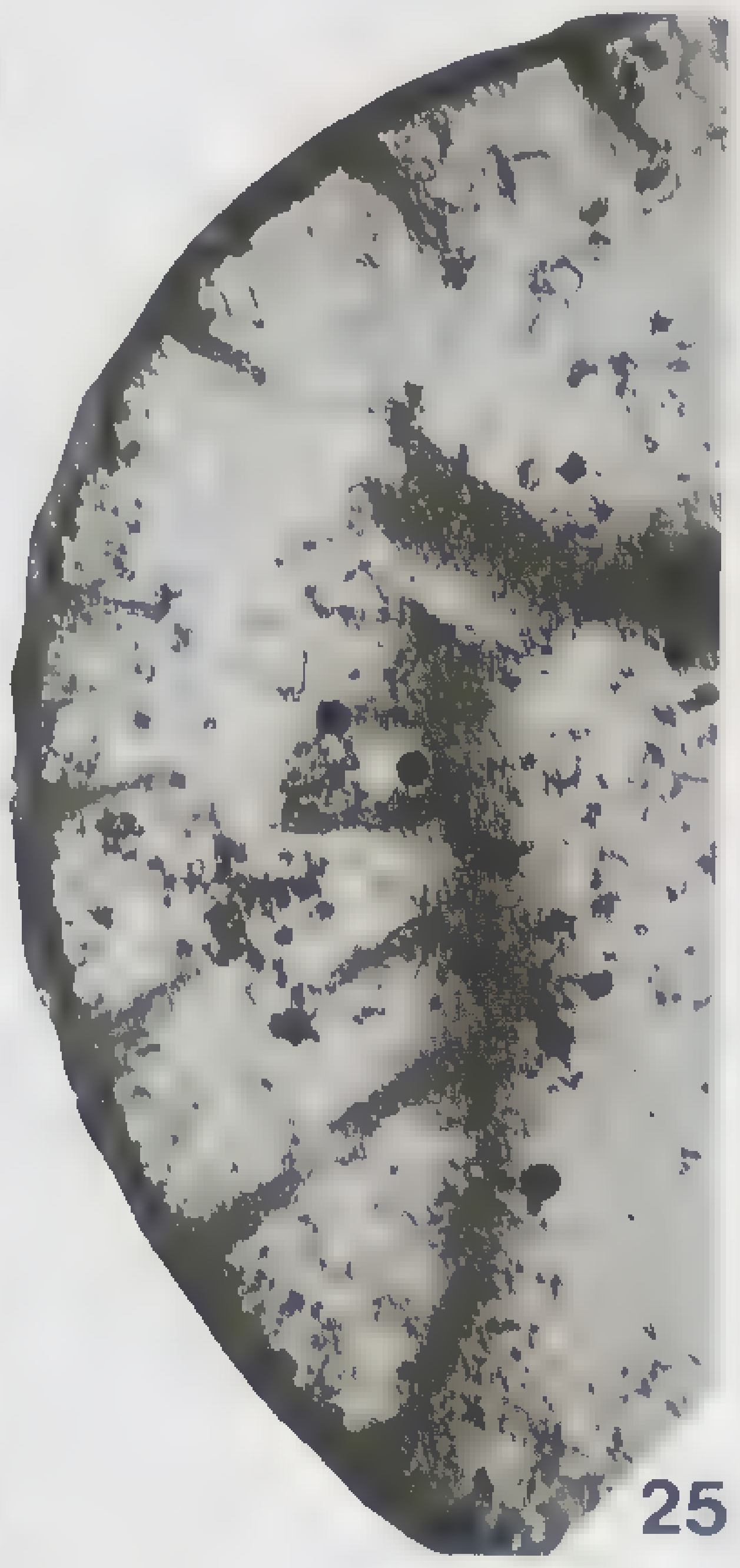
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Order **ORTHIDA**
Schuchert and Cooper, 1932

Family **DALMANELLIDAE**
Schuchert, 1913

Genus **LEVENEA**
Schuchert and Cooper, 1931

Type species.- - -Orthis subcarinata Hall, 1857, p. 43.

Levenea subcarinata (Hall, 1857)

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Pentagonia unisulcata (Conrad, 1841)

Plate 6, figures 7- -13

Atrypa unisulcata Conrad, 1841, p. 56.

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Meristella? *unisulcata* (Conrad). Hall, 1862, p.158, pl. 2, figs. 17, 20--23 (not figs. 19, 24, 25).
Non *Meristella unisulcata* (Conrad). Nettleroth, 1889, p. 99, pl. 15, figs. 9--16.
Pentagonia unisulcata (Conrad). Stauffer, 1915, p. 104, 245 (not pp. 160, 171, 175, 234); Goldring, 1935, p. 148, figs. 53B--D.

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1979. Recognition of ancestor-descendant relationships in invertebrate paleontology. *in* Phylogenetic analysis and paleontology. J. Cracraft and N. Eldredge, *eds*., Columbia University Press, New York, pp. 113--164.

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Book, single author:

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1968. Search for the past. An introduction to paleontology. 2nd edition. Prentice-Hall, Englewood Cliffs, NJ, 512 pp.

Book, multiple authors:

Fretter, V., and Graham, A.

1962. British prosobranch molluscs. Ray Society, London, 755 pp.

Dissertation or thesis:

Allison, R. C.

1967. The Cenozoic stratigraphy of Chiapas, Mexico, with discussion of the classification of the Turritellidae and selected Mexican representatives. unpublished PhD thesis, University of California, Berkeley, 450 pp.

Paper presented at meeting:

Allmon, W. D.

1987. Multiple modes of homeomorphy in Cenozoic turritellid gastropods and their evolutionary implications. Geological

Society of America, Abstracts with Programs, vol. 19, no. 7, p. 570.

Treatise on Invertebrate Paleontology

Cox, L.

1960. General characteristics of Gastropoda. *in* Treatise on invertebrate paleontology. R. C. Moore, *ed.*, Part I, Mollusca 1, by J. B.Knight *et al.*, Geological Society of America and University of Kansas Press, pp. I84--I169.

Field guides:

Beauchamp, R. G.

1984. Stratigraphy and depositional environments of the Brightseat and Aquia Formations, Maryland and Virginia. *in* Cretaceous and Tertiary stratigraphy, paleontology and structure, southwestern Maryland and northeastern Virginia. American Association of Stratigraphic Palynologists Field Trip Guidebook. N. O. Fredericksen and K. Kraft, *eds.*, pp. 78--111.

INDEX

Each issue of both *Bulletins of American Paleontology* and *Palaeontographica Americana* includes an index. Construction of the index is the responsibility of the author(s) and is requested at page proof stage.

ILLUSTRATIONS AND TABLES

High-quality illustrations have been a hallmark of both *Bulletins of American Paleontology* and *Palaeontographica Americana* since their inception and are expected of all manuscripts.

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Prepare text-figures for reproduction as single column (82 mm; 3¼ inches) or two column (178 mm; 7 inches) width. All text-figures should be prepared so as to be read with the journal in normal reading position (*i.e.*, if illustrations must be more than 7″ wide, consider putting them on two facing pages; if 14″ is not wide enough, consider recasting the illustration as a foldout.

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A foldout may be particularly helpful for stratigraphic range data, *e.g.,* taxa arising in stratigraphic order if there is a clear trend, or, if such a trend is not present, alphabetically by genus, and within that by species. In this way, individual taxa can be much more easily located, and their "bedmates" more comfortably comprehended. Such charts can be published as foldouts. Foldouts must be drafted to be no more than 9″ high, but they may be up to 25″ wide. These are inserted inside the front or back covers, and nothing is printed on the first fold, so that the foldout can be viewed while reading the monograph, without having to flip back and forth.

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Tables should be prepared one to a page. Table captions should be prepared separately, one to a page. Avoid vertical lines in Tables. Use abbreviations in tables as little as possible, and define, in the INTRODUCTION TO SYSTEMATIC PALEONTOLOGY (see above) any you must use that might be ambiguous.

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Authors are required to defray a portion of the costs of publication. These costs are assessed not as page charges, but rather on the basis of illustrations. Currently, the following cost schedule is in effect:

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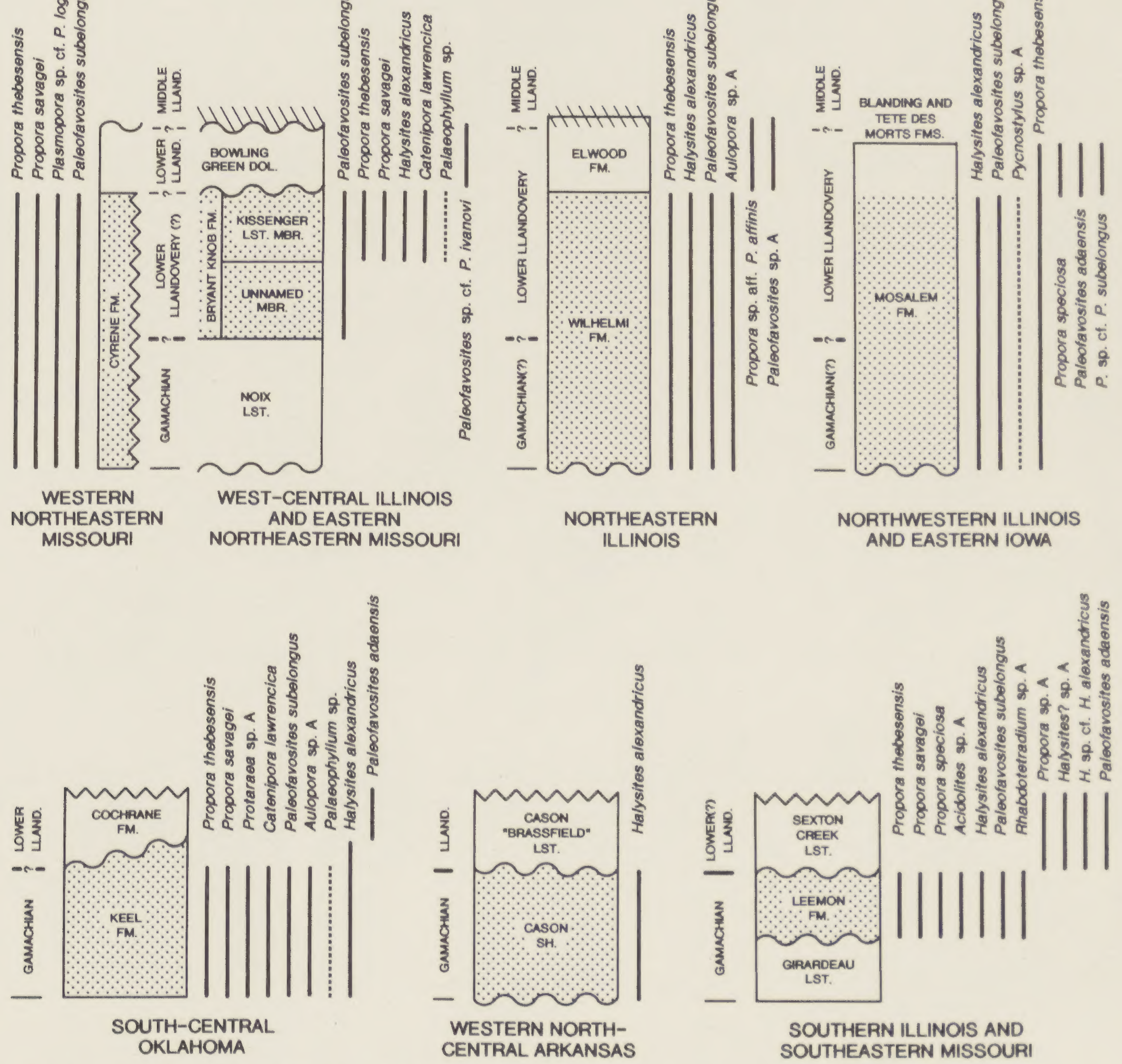

Propora thebesensis
Propora savagei
Plasmopora sp. cf. P. logani
Paleofavosites subelongus
CYRENE FM.
GAMACHIAN
LOWER LLANDOVERY (?)
LOWER LLAND.
MIDDLE LLAND.
WESTERN NORTHEASTERN MISSOURI
BOWLING GREEN DOL.
KISSENGER LST. MBR.
UNNAMED MBR.
BRYANT KNOB FM.
NOIX LST.
Paleofavosites subelongus
Propora thebesensis
Propora savagei
Halysites alexandricus
Catenipora lawrencica
Palaeophyllum sp.
Paleofavosites sp. cf. P. ivanovi
WEST-CENTRAL ILLINOIS AND EASTERN NORTHEASTERN MISSOURI
GAMACHIAN(?)
LOWER LLANDOVERY
MIDDLE LLAND.
ELWOOD FM.
WILHELMI FM.
Propora thebesensis
Halysites alexandricus
Paleofavosites subelongus
Aulopora sp. A
Propora sp. aff. P. affinis
Paleofavosites sp. A
NORTHEASTERN ILLINOIS
GAMACHIAN(?)
LOWER LLANDOVERY
MIDDLE LLAND.
BLANDING AND TETE DES MORTS FMS.
MOSALEM FM.
Halysites alexandricus
Paleofavosites subelongus
Pycnostylus sp. A
Propora thebesensis
Propora speciosa
Paleofavosites adaensis
P. sp. cf. P. subelongus
NORTHWESTERN ILLINOIS AND EASTERN IOWA
GAMACHIAN
LOWER LLAND.
COCHRANE FM.
KEEL FM.
Propora thebesensis
Propora savagei
Protaraea sp. A
Catenipora lawrencica
Paleofavosites subelongus
Aulopora sp. A
Palaeophyllum sp.
Halysites alexandricus
Paleofavosites adaensis
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GAMACHIAN
LLAND.
CASON "BRASSFIELD" LST.
CASON SH.
Halysites alexandricus
WESTERN NORTH-CENTRAL ARKANSAS
GAMACHIAN
LOWER(?) LLAND.
SEXTON CREEK LST.
LEEMON FM.
GIRARDEAU LST.
Propora thebesensis
Propora savagei
Propora speciosa
Acidolites sp. A
Halysites alexandricus
Paleofavosites subelongus
Rhabdotetradium sp. A
Propora sp. A
Halysites? sp. A
H. sp. cf. H. alexandricus
Paleofavosites adaensis
SOUTHERN ILLINOIS AND SOUTHEASTERN MISSOURI

Text-figure 8.—Composite stratigraphic sections showing uppermost Ordovician (Gamachian) and lowermost Silurian (Llandovery) units and distribution of colonial corals in the east-central United States (see Text-fig. 1A, foldout inside front cover). Thicknesses of units are not to scale. Range lines of species (solid for Tabulata, dotted for Rugosa) indicate presence within, but not necessarily throughout, the intervals indicated (for details, see Text-figs. 2–7 and text). Strata containing colonial corals of the Edgewood Assemblage are stippled; colonial corals in overlying strata represent the Silurian assemblage. Hachures indicate the *Platymerella manniensis* zone.

PREPARATION OF MANUSCRIPTS

Bulletins of American Paleontology usually comprises two or more separate papers in two volumes each year. The series is a publication outlet for significant, longer paleontological monographs (*i.e.*, more than approximately 50 printed pages), for which high quality photographic illustrations and the large quarto format are required.

Submissions are welcome from any author, regardless of institutional or organizational affiliation. Authors must, however, be members of the Paleontological Research Institution at time of publication; annual membership is currently US$25.00. Publication costs of the *Bulletins* are heavily subsidized by the Institution, but authors are currently required to pay illustration charges at a rate of $120.00 per plate and $35.00 per text-figure.

Important references for style and format are 1) *Bulletins of American Paleontology* "Instructions for Authors" (volume 108, number 347, pages 149–153); 2) *Chicago Manual of Style* (fourteenth edition) 1993. Recent issues of the *Bulletins* provide useful guides but note changes with the "Instructions for Authors" mentioned above.

Manuscripts must be typewritten, and double-spaced *throughout* (including direct quotations, tables and references). All manuscripts should contain a table of contents, lists of text-figures and/or tables, and a short, informative abstract that includes names of all new taxa. Format should follow that of recent numbers in the series. All measurements must be given in the metric system, alone or in addition to their English system equivalents. The maximum dimensions for photographic plates are 178 mm × 229 mm (7 inches × 9 inches; outlined on this page). Single-page text-figures should be drafted for reproduction as single column (82 mm; 3¼ inches) or full page (178 mm; 7 inches) width, but arrangements can be made to publish text-figures that must be larger.

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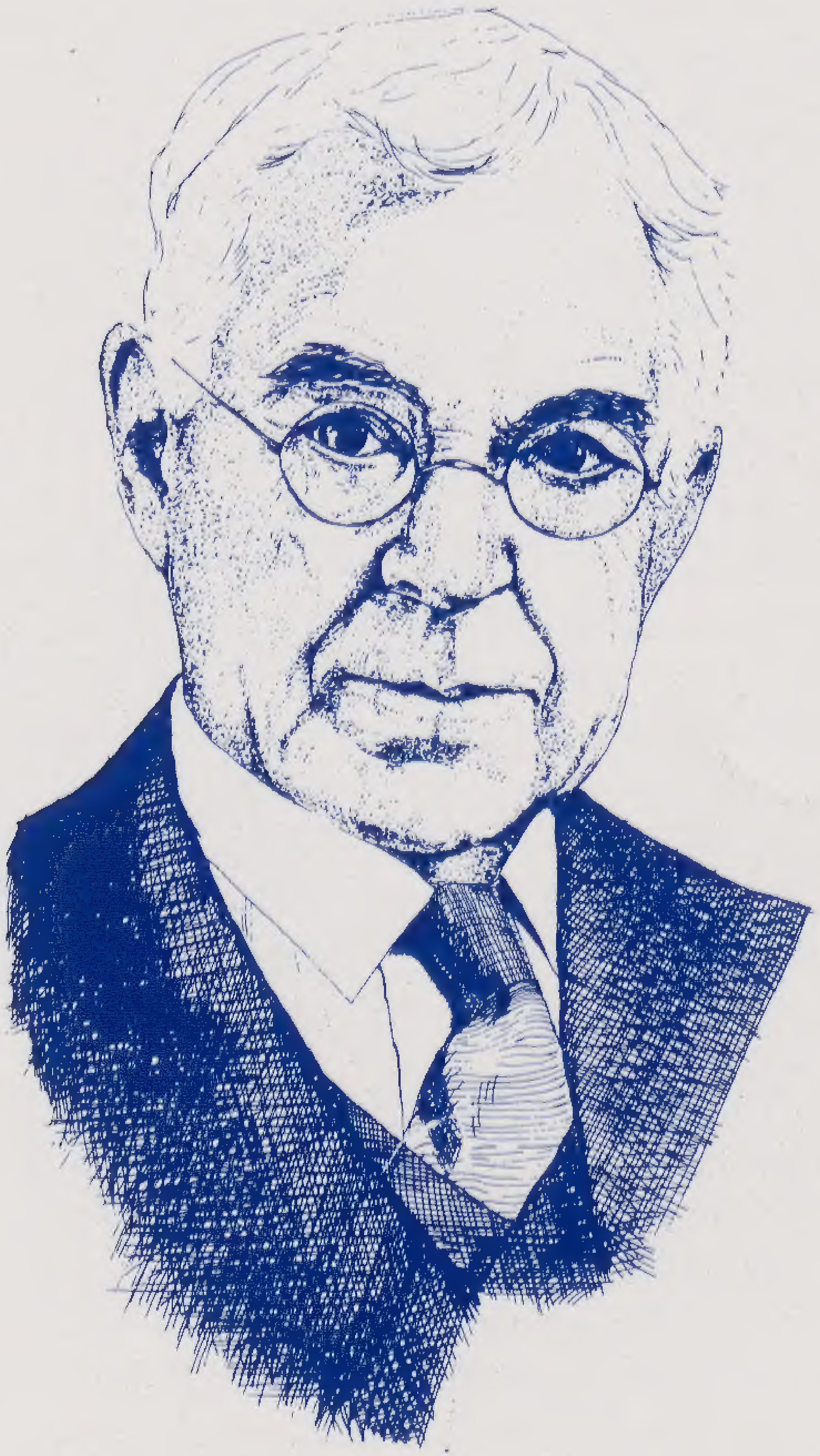

Gilbert Dennison Harris
(1864 - 1952)

Founder of the *Bulletins of American Paleontology* (1895)

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